STUDIES IN THE GENUS

<u>LUZULA</u>

Thesis submitted for the degree of Doctor of Philosophy

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STUDIES IN THE GENUS *LUZULA* DC.

INTRODUCTION

The genus *Luzula* DC. is the second largest in the family Juncaceae. In the Pflanzenreich monograph of the family the author, F. von Buchenau, described 61 species. This compares with 1 species each in the genera *Patosia*, *Rostkovia* and *Priomium*, 2 in *Oxychloe* and 3 in *Distichia* and *Marsippospermum*; *Juncus*, by far the largest genus, comtained 207 species.

The six smaller genera are all confined to the southern hemisphere, while *Luzula* and *Juncus*, though both cosmopolitan, are both more abundant in the temperate regions of the northern hemisphere than they are elsewhere.

Distichia, *Patosia* and *Oxychloe* are all exclusively South American genera, occurring mainly in the Andes. *Marsippospermum* has one species, *M.reichii*, confined to Patagonia; another, *M.grandiflorum*, comes from Patagonia, Tierra del Fuego and the Falkland Islands, while the third, *M.gracile*, is found in mountainous regions of New Zealand, and in the Aukland and Campbell Islands. *Rostkovia* occurs in Patagonia, Tierra del Fuego, the Falkland Islands, South Georgia, the South Island of New Zealand and on Campbell Island. *Prionium* is found only in the Cape region of South Africa.

The presence of these small, and possibly relic, genera only in the southern hemisphere may indicate that the family had its origins in that region. The two more successful genera, *Luzula* and *Juncus* might then have spread northwards to cover the greater part of the globe, from the tropics to the Arctic and Antarctic.

Linnaeus described, in the Species Plantarum (1753), such species in the genus Luzula as were known to him, but included them in the genus Juncus. The name Luzula was first used by Lamarck and De Candolle in the Flore Française ~~de la France~~, published in 1805. Previously in 1763, however, the name Juncoides had been applied by Adams to this group of plants. After 1805 the name Luzula was used mainly in Europe, while American botanists used the earlier name, Juncoides. In the 1950 International Code of Nomenclature, Luzula is cited as a nomen conservandum, with Luzula campestris (L.) DC. as the type species.

Luzula is divided into three subgenera:-

Pterodes, with 9 spp.

Anthelaea, with 16 spp.

Luzula (Gymnodes), with 36 spp.

Subgenus Pterodes contains the British species L.pilosa and L.forsteri. In it the flowers are borne singly on the stalks of the branched inflorescence. The seeds have a caruncle at the apex; this may be large, and is frequently hooked.

The subgenus Anthelaea contains the British species L.sylvatica; the inflorescence is much branched, the flowers being borne in small clusters at the end of the branches. The seeds have no caruncle, but usually carry a small tuft of fibrils at the base.

The subgenus _Luzula_ includes _L.campestris_, _L.spicata_ and _L.arcuata_. The inflorescence is less branched than in the other two subgenera, the flowers occurring in more or less dense heads or clusters. They may be in a lax or congested inflorescence. The seed often has a basal caruncle, though this is absent in some species.

See fig. 1.

Buchenau arranges related species in groups in his monograph. These are, however, very general, and show only a vague circle of affinity, and it appears that in many cases a species has as close, or closer, relatives in another group. In some cases hybrids are recorded between species of different groups, which appear, therefore, to be somewhat arbitrary.

One group of related species in the monograph includes the following:-

L. modesta Buchenau

L. leptophylla Buchenau et Petrie

L. wettsteinii Buchenau

L. rhadina Buchenau

L. longiflora Benth.

L. hawaiiensis Buchenau

L. africana Drège

L. comosa E. Mey.

L. campestris DC.

The first four are all small plants confined to Tasmania or New Zealand. *L.longiflora* is found only on Lord Howes Island, *L.hawaiiensis* in Hawaii, and *L.africana* in South Africa. *L.comosa* occurs in the North-Western states of America, and in western Canada. *L.campestris*, in the sense that Buchenau employed the name, is an almost cosmopolitan species, largely occurring in the northern and southern temperate zones; it was divided by Buchenau into 20 varieties. It is this species, with its 20 varieties, and also some of the other closely related species, which forms the subject of this investigation.

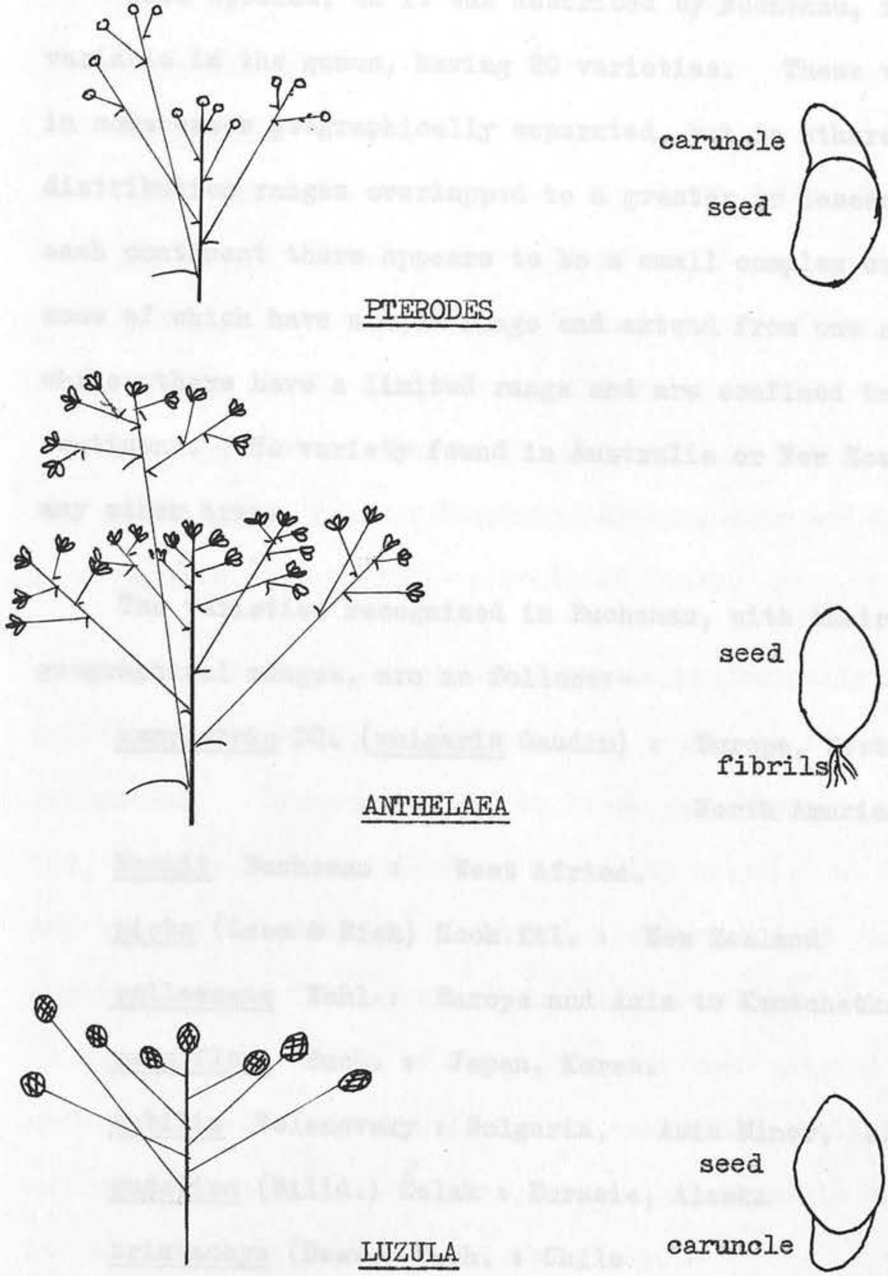

Fig. 1. Diagram of the inflorescences and seeds of the sub-genera in the genus *Luzula*.

I. LUZULA CAMPESTRIS s.l.

This species, as it was described by Buchenau, is the most variable in the genus, having 20 varieties. These varieties were in some cases geographically separated, but in others the distribution ranges overlapped to a greater or lesser extent. In each continent there appears to be a small complex or varieties, some of which have a wide range and extend from one area to another, while others have a limited range and are confined to only one continent. No variety found in Australia or New Zealand extends to any other area.

The varieties recognised in Buchenau, with their approximate geographical ranges, are as follows:-

campestris DC. (vulgaris Gaudin) : Europe, Western Asia North America.

Mannii Buchenau : West Africa.

picta (Less.& Rich) Hook.fil. : New Zealand

pallescens Wahl.: Europe and Asia to Kamtchatka.

pauciflora Buch. : Japan, Korea.

debilis Velenovsky : Bulgaria, Asia Minor, Altai.

sudetica (Willd.) Čelak : Eurasia, Alaska

tristachya (Desv.) Buch. : Chile

Banksiana (E. Mey) Buch. : New Zealand

congesta (Thuill.) Buch. : Central and Western Europe, South Greenland.

australasica (Steud.) Buch. : New Zealand, Tasmania and New South Wales.

capitata Miq. : Japan, Korea.

Petrieana Buch. : New Zealand.

flaccida Buch. : Tasmania, New South Wales, Fiji.

floribunda Buch. : New Zealand.

crinita (Hook.f.) Buch. : Islands south of New Zealand.

frigida Buch. : Arctic and subarctic America and Eurasia.

migrata Buch. : Australia, Tasmania and New Zealand.

multiflora Čelak. : Temperate Europe, Asia and North America.

calabra (Ten.) Buch. : South of Italy.

On the whole, the varieties are morphologically distinct, but individual plants may be difficult to assign to any one of the above categories. These intermediate forms are, however, surprisingly few, judging from the existing herbarium material at Edinburgh, Kew and the British Museum. If these taxa are indeed varieties, one might expect to find more intermediate specimens than seem, in fact, to exist. The status of these taxa has been altered by various authors; in the regional floras of the world, published both before and after Buchenau's monograph, there is remarkable lack of uniformity in the taxinomic treatment of the group.

Buchenau in 1906 treated all the taxa as having the same rank, namely the variety. In his previous monograph, published in 1890, his treatment was less uniform, the taxa ranging from species, through subspecies to variety. This varied treatment was in common with that of other authors, who considered some of the taxa as being more closely allied to each other than to the remainder of the group. For example, in Koch's Flora Germanicae et Helveticae (1843), L.campestris and L.multiflora were described as distinct species, while congesta and pallescens were treated as varieties of multiflora.

Since 1906, when the Pflanzenreich monograph was published, the status of some of the varieties has been raised by various authors, and few would now treat all members of the complex as varieties of a single species. The treatment of the group has, however, been so confused that a more thorough revision of the whole complex throughout the world seems desirable.

The most logical point at which to start a revision would seem to be Buchenau's 1906 monograph, although a few taxa have been added to the group since then. The taxa will be referred to by the specific or varietal epithet only, with no indication as to rank, which is dealt with in chapter VII of this thesis. The first step would seem to be to establish the reality of all the taxa described, by consulting the herbarium material at Edinburgh, Kew and the British Museum.

The taxa which have been examined are keyed out and listed below, together with a short description of each; where possible, a photograph is included of a dissection of a flower. These photographs were taken using the actual dissections as negatives. The flowers were boiled in water and dissected on a slide in the usual way, but instead of being mounted on a card the perianth segments, stamens and carpel walls were mounted in a clear mountant on a slide, and covered with a cover slip. Because of their thickness, the seeds had to be mounted separately, and were not covered. The slides were then put into the enlarger and used as ordinary negative material.

The resulting prints have the appearance of a negative, but prints from them, using duplicating paper, resulted in too much loss of detail.

KEY TO THE TAXA

1. Inflorescence spicate 2

   Inflorescence capitulate 3

2. Stems 10 to 20 cms.; N. America .... *cusickii*

   Stems c. 40 cms.; S. Italy .... *calabra*

3. Plant slightly stoloniferous at base 4

   Plant caespitose, or slightly bulbous at base 6

4. Plants small, rarely more than 20 cms. high; inflorescence with 4-5 heads, the stalks often curved downwards; perianth 3 - 4 mm....................... *campestris*

   Plants 15 to 30 cms.; rarely smaller, branches of the inflorescence erect 5

5. Leaves broad, 5 - 7 mm.; inflorescence with 5 - 8 heads, each about 1 cm. across; flowers brown, 3 - 3.5 mm.. *mannii*

   Leaves narrow, 1.5 - 3 mm.; inflorescence much branched with numerous heads; flowers 2.5 - 3 mm., perianth segments scarious at edges with dark stripe down centre .... *picta*

6. Inflorescence lax 7

   Inflorescence congested, but sometimes with one or two of the lower heads stalked 18

7. Flowers very small, less than 2.5 mm................ 8

   Flowers more than 2.5 mm. long 10

8. Plant bulbous at base, perianth 2 - 2.3 mm. (N. America) .... *bulbosa*

   Plant not bulbous, flowers usually less than 2 mm... 9

9. Heads with many flowers; perianth very pale ..... pallescens

Heads with few flowers; perianth brown .... pauciflora

10. Plants very small, rarely more than 10 cms........ 11

Plants usually over 10 cms. 12

11. Stems erect; perianth dark brown (New Zealand) .. petrieana

Stems flaccid; perianth pale and membrous (Australia) .... flaccida

12. Upper branches of the inflorescence reflexed, or strongly divergent 13

All branches of the inflorescence erect 14

13. Plant slightly bulbous at base (Australia) .... migrata

Plant not bulbous at base (N. America) .... echinata

14. Leaves densely hairy; stems robust (New Zealand). 15

Leaves slightly dairy; stems slender 16

15. Inflorescence very much branched, with up to 50 heads; leaves 3 - 7 mm. broad .... floribunda

Inflorescence umbellate, heads not numerous; leaves about 4 mm. broad .... crinita

16. Stems 10 to 15 cm.; flowers 2 - 3 mm., dark brown. frigida

Stems over 15 cm. 17

17. Flowers very large (c. 4 mm.) dark brown; leaves about 5 mm. broad .... kobaysii

Flowers medium size, 2 - 3.5 mm., brown; leaves (1.5-)2 - 4(-4.5) mm. broad .... multiflora

18. Flowers very small, about 2 mm., dark brown 19

Flowers about 3 mm. or more, dark or light brown . 20

19. Plant small, about 10 cm.; leaves about 4 mm. broad (Aleutians) .... <u>kjellmanniana</u>

Plant 15 to 30 cm.; leaves 2 - 3 mm. broad ...... <u>sudetica</u>

20. Flowers very large, usually 4 mm. or more 21

Flowers (2-) 2.5 - 3.5 (-4) mm. 22

21. Leaves equalling or exceeding stem, up to 7 mm. broad and densely hairy; perianth segments dark at centre with pale margins (New Zealand) .... <u>Banksiana</u>

Leaves shorter than the stem, c. 5 mm. broad, sparsely hairy; perianth segments dark brown .... <u>kobaysii</u>

22. Stems usually over 30 cm. high; perianth brown, 3 - 4 mm .... <u>congesta</u>

Stems less than 30 cm. 23

23. Leaves broad, c. 4 mm., densely hairy .... <u>crinita</u>

Leaves 3 mm. or less 24

24. Plant small, less than 15 cm. (Australia) .... <u>australasica</u>

Plant taller, usually over 15 cm. 25

25. Leaves 2.5 - 3 mm. broad (Chile) .... <u>tristachya</u>

Leaves (2.5-) 3 - 4 (-4.5) mm. broad (Japan) ..... <u>capitata</u>

1. campestris (vulgaris) :- Stem 3 - 25 cm. high, stoloniferous at base; leaves narrow, 2 - 10 (12) cm. long, (0.10-) 0.20 - 0.25 (-0.35) cm. wide. Inflorescence with 3 - 5 heads, the stalks of which are often curved downwards; flowers 3 - 3.5 mm. long, perianth dark brown; anthers $^2/_3$ total length of the stamen; seed more or less spherical, with a basal caruncle.

2. Mannii :- Stem 20 - 35 cm; leaves up to 25 cm. long, 0.5 - 0.7 cm. broad. Inflorescence rather lax, the flowers borne in 5 - 8 almost spherical heads, each about 1 cm. across; flowers dark brown, 3.0 - 3.5 mm. long; capsules shorter than the perianth.

3. picta :- Stem slender, 10 - 30 cm; leaves long and rather narrow, up to 0.25 cm. broad. Inflorescence lax, the flowers borne in small clusters on erect stalks; flowers about 3.0 mm. long, the perianth segments rather long and narrow, with pale margins and a dark brown midrib; seeds ovoid.

4. pallescens :- Stem slender, 10 -30 cm; leaves 7 - 17 cm. long, rather narrow, 0.20 - 0.35 cm. broad, usually about 0.25 cm. Inflorescence generally much branched, with up to 20 heads; flowers very small, about 2 mm. long, pale yellowish brown in colour; anther more or less the same length as the filament; seeds small, ovoid.

5. pauciflora :- Stem 15 - 30 cm; leaves about 10 cm. long, and up to 0.4 cm. broad. Inflorescence lax, with 4 - 12 heads; flowers small, about 2.0 - 2.5 mm. long, the perianth segments dark brown with narrow membranous margins; seeds ovoid, nearly twice as long as broad.

6. debilis :- Very similar to sudetica, but differs, according to Buchenau, in having perianth segments with membranous tips, and which are much longer than the ripe capsule (in sudetica they are completely brown and shorter than the capsule).

7. sudetica :- Stem 10 - 35 cm; leaves 5 - 15 cm. long, 0.25 - 0.3 (-0.45) cm. broad. Inflorescence usually congested, but occasionally lax, or with only one or two stalked heads; flowers very small, in dense clusters; perianth segments dark brown, about 2 mm. long, shorter than or equalling the capsule; seeds ovoid, small.

8. tristachya :- Stem 10 - 30 cm; leaves 5 - 12 cm. long, and up to 0.30 cm. broad. Inflorescence congested, with 3 - 5 heads; perianth segments dark brown, about 3.5 mm. long, with membranous margins; capsule slightly shorter than the perianth; seeds broadly ovoid.

9. Banksiana :- Stem very stiff and thick, up to 20 cm. high; leaves about 10 cm. long, and up to 0.70 cm. broad,

densely hairy at the margins. Inflorescence congested, with 2 or 3 large, very hairy bracts subtending the lower heads; flowers brown, about 4.0 mm. long.

10. congesta :- Stems 15 - 60 (-70) cm; leaves 5 - 20 cm. long, and up to 0.60 cm. broad, usually 0.30 - 0.35 cm. Inflorescence congested, but sometimes with 1, or even 2, stalked heads; 3 - 4 mm. long; capsule shorter than the perianth; seeds ovoid, rather large.

11. australasica :- Stems 7 - 15 cm. Inflorescence usually congested, conical or lobed; flowers darkish brown, about 3.0 mm. long; seeds broadly ovoid.

12. capitata :- Stem 7 - 35 cm; leaves 5 - 12 cm. long, 0.25 - 0.50 cm. broad. Inflorescence congested, but sometimes with one stalked head; flowers brown, 3.0 - 3.5 mm. long; seeds ovoid.

13. petrieana :- Stems 10 - 20 cm; leaves about 0.2 cm. broad, somewhat inrolled. Inflorescence congested or lax; flowers dark brown.

14. flaccida :- Stems 10 (-20) cm; leaves long and narrow, flaccid. Inflorescence small, usually lax but sometimes congested; flowers 2.5 - 3.0 mm. long, very pale, usually longer than the fruit. The whole plant is very pale and slender. (Description from Buchenau, as no specimen was

examined which fitted this category; it seems possible that it is a shade form.)

15. floribunda :- Stem 25 - 40 cm; leaves rather long and broad. Inflorescence lax, very much branched, with up to 50 heads; flowers about 3.0 mm. long, rather light brown.

16. crinita :- Stems rather short and stiff, 5 - 20 cm; leaves about 10 cm. long, and 0.4 - 0.5 cm. broad, densely hairy at the margine. Inflorescence congested, with numerous flowers; flowers brown, 2.0 - 3.0 mm. long. Very like banksiana, but the flowers are smaller.

17. frigida :- Stem 5 - 30 cm., usually about 15 cm; leaves 3 - 13 cm. long, 0.15 - 0.40 cm. broad; both leaves and stem are often red in colour. Inflorescence usually lax, the branches rather short and stiff, sometimes congested; flowers 2.3 - 3.5 mm. long, dark brown, longer than the capsule; seeds ovoid.

18. migrata :- Stems usually 10 - 25 cm., sometimes bulbous at the base; leaves rather short, but may be up to 10 cm. long, 0.20 - 0.30 mm. broad. Inflorescence lax, the lower branches more or less erect, the upper ones somewhat deflexed; flowers brown, 2.0 - 3.0 mm. long; seeds ovoid.

19. multiflora :- Stems 12 - 60 cm; leaves 5 - 22 cm. long, (0.15-) 0.20 - 0.40 (-0.60) cm. broad. Inflorescence lax, with 3 - 10 heads, usually 5 - 8; flowers brown, 2.0 - 4.0 mm. long, usually about 3.0 mm; seeds ovoid, smaller than those of congesta.

20. calabra :- Stems slender, about 40 cm; leaves narrow, about 0.20 cm. broad. Inflorescence spicate, with erect branches; flowers 2.0 - 2.5 cm. long, brown. (From Buchenau's description, as no specimens of this taxon were available.)

21. echinata :- Stem 10 - 20 cm; leaves 2 - 7 cm. long, up to 0.30 cm. broad. Inflorescence lax, the branches strongly divergent, some more or less reflexed, as in migrata; heads hemispherical; flowers brown, 3.0 - 4.0 mm. long, considerably exceeding the capsule.

22. bulbosa :- Stem 10 - 20 cm., bulbous at the base; leaves 3.0 - 5.5 cm. long, up to 0.30 cm. broad. Inflorescence lax, the branches more or less erect; flowers brown, 2.0 - 2.5 mm. long, equalling or shorter than the capsule.

23. comosa :- Stem 10 - 30 (-40) cm; leaves up to 15 cm. long and 0.30 - 0.50 cm. broad. Inflorescence lax or congested, if congested, then more or less spicate; flowers 3.0 - 4.5 mm. long, rather dark brown, usually longer than the capsule;

seeds ovoid.

var. macrantha :- Flowers 5.0 - 6.5 mm. long.

24. kobaysii :- Plant very large and rebust; leaves broad, c. 5 mm. Inflorescence usually lax, sometimes congested; flowers dark brown, c. 4 mm. long.

25. kjellmanniana :- Plant small, c. 10 cm. high; leaves rather brown, c. 4 mm. Inflorescence congested; flowers dark brown, about 2 mm.

26. cusickii :- Plant small and slender. Inflorescence spicate; flowers dark brown.

Photographs of dissections of flowers of the following taxa are shown in plates 1 - 16. -
australasica, banksiana, bulbosa, campestris, capitata, comosa, congesta, echinata, frigida, migrata, multiflora, pallescens, pauciflora, picta, sudetica.

Nearly all of the taxa in the Luzula campestris species complex which have been described in the literature have been examined in the form of herbarium specimens. No material of debilis was available under that name, but several specimens from eastern Europe and from Asia Minor may fit into this category; its exact delimitation and distinction from sudetica is doubtful, but insufficient material was available to come to any decision as to its status.

No material of calabra was examined, and no specimens fitting its description were found at any of the herbaria.

The vast majority of specimens of migrata from Australia and New Zealand were labelled simply "Luzula campestris". As they were obviously not campestris s.s., it was necessary to find to which of the taxa they belonged. Examination of the monograph and other literature indicated that most of these plants belonged to Buchenau's var. migrata, though none of these descriptions was very full. Only one specimen (at Kew) in the three herbaria was labelled migrata ; it was collected by Lester - Garland in 1926 at Nietta, in northern Tasmania, and is labelled "L. campestris ? var. migrata".

Specimens of L. campestris from the Blue Mountains in Oregon collected by Cusick in 1899 bear the number 2248, which is the same as that cited in the description of var. Cusickii Gaud.; these specimens are presumably isotypes.

II. GEOGRAPHICAL DISTRIBUTION

Maps showing the geographical distribution of most of the taxa in the group have been constructed. The data were derived from a) herbarium material, b) the available literature (regional floras of the world, etc.) ~~and~~ when it seemed sufficiently reliable for the taxon concerned. In the maps, the dots indicate individual herbarium specimens or gatherings; the line surrounding the dots indicates the probable limits of distribution of the taxon in question, estimated from herbarium material, and from its occurrence recorded in various regional floras, covering as large an area of the world as possible. The information from the literature is perhaps not always very reliable, owing to the lack of uniformity in the treatment of the group as a whole.

The following taxa have been included in the maps, (figs. 2 - 7) several being put on the one map, with as little overlap of areas as possible.

acadiensis	2	cusickii	7	migrata	5
australasica	3	echinata	3	multiflora	5
banksiana	3	floribunda	7	oahuensis	5
bulbosa	4	frigida	6	pallescens	2
campestris	3	hawaiiensis	2	pauciflora	3
capitata	6	kjellmanniana	4	petrieana	6
comosa	2	kobaysii	5	picta	2
congesta	4	longiflora	4	sudetica	7
crinita	4	mannii	6	tristachya	6

The herbarium material at Edinburgh, Kew and the British Museum was examined, also some specimens lent by the National Herbarium of New South Wales.

The maps show that most of the taxa are found in the northern hemisphere, in temperate and arctic regions; several of these have a wide distribution across Europe and northern Asia, sometimes extending to North America as well. Other taxa have a most limited distribution, especially those in North America and in the region of Japan and Korea. No single taxon occurs in both northern and southern hemispheres, and the taxa in the south have an even more limited distribution than those in the north, none occurring in more than one continent. There is a small complex in Australia and New Zealand, and neighbouring islands, consisting of seven taxa; two of these, australasica and migrata, are common to Australia and New Zealand. In Africa, a very distinct taxon, mannii is found in the Cameroons, while the related species L. africana Drège occurs in south and eastern Africa. Specimens from parts of Southern Africa bear a strong resemblance to the European multiflora, and are possibly introduced. In South America there is a single, distinct taxon, tristachya.

campestris s.s. :- Europe and Asia Minor. In Europe, it is abundant in western and central regions, extending south to Spain, Italy and Greece, and also to Turkey. In the north, the range is from the Faroes, through the south of Norway and Sweden, to Russia west of the Urals. Specimens from the Himalayan region have been referred to this taxon, but their position in the group is somewhat doubtful, as they appear in some respects to be intermediate between campestris and multiflora, though possibly resembling the former more closely.

multiflora :- The most widespread of all the taxa, it extends right round the world in the north temperate and subarctic regions. It is abundant in Europe, from the Mediterranean to the north of Scandinavia; it occurs in Iceland, S. Greenland and over most of North America, except the extreme north, and the drier central areas of the United States. It is found in the Aleutian Islands, and extends through Kamtchatka to Japan and Korea. In Asia the range is slightly more southern, the plant being found mainly in the Himalaya and the Altai.

congesta :- Western and central Europe, extending to the Purenees and Alps; possibly also occurs in Turkey. Specimens from the Azores, Labrador and south Greenland are also referred to this taxon, which has been much confused in the literature.

pallescens :- A more easterly distribution; it is found in north and central Europe, and across Asia to Kamtchatka. The taxon extends to the north of Scandinavia, while its western limit is in the south-east of England, where it is native only near Huntingdon.

sudetica :- Has an arctic-alpine distribution. It occurs in the arctic and subarctic regions of Europe and Asia, and extends to Alaska, but not across the continent of North America. It is present in Iceland, but appears to be absent from Greenland. In more southerly latitudes it is found in the mountainous areas of Europe and Asia, including the Alps, Pyrenees, Caucasus and Altai.

frigida :- Has a more arctic-subarctic distribution then *sudetica*, and occurs in the north of Asia, the northern half of Scandinavia, Iceland, south Greenland, Labrador, northern Canada, Alaska and the Aleutians. It appears to be absent from Kamtchatka and the east of northern Asia.

echinata :- South-eastern part of the United States, but does not extend into Florida.

bulbosa :- Similar distribution to *echinata*, but extends somewhat farther westwards, round the Gulf of Mexica.

comosa :- North-western states of the United States, and in British Columbia. It extends, in a belt more or less parallel to the coast, from California to north of Vancouver.

acadiensis :- Limited to Prince Edward Island, off the east coast of Canada.

cusickii :- Recorded only from the Blue Mountains in Oregon.

<u>australasica</u> :- South-eastern part of Australia, Tasmania, and in the North and South Islands of New Zealand.

<u>crinita</u> :- Lord Aukland's Island, Campbell Island and Macquarie Island, all of which lie to the south of New Zealand.

<u>banksiana</u> :- Only on Dog Island, at the southern tip of the South Island of New Zealand.

<u>petrieana</u> :- Mountain regions of New Zealand.

<u>picta</u> :- North and South Islands of New Zealand.

<u>migrata</u> :- The most widely distributed of the Australia-New Zealand complex, it is recorded from south-western and south-eastern Australia, Tasmania and both islands of New Zealand. On the east coast of Australia it extends considerably farther north than does <u>australasica</u>.

<u>floribunda</u> :- South Island of New Zealand.

<u>capitata</u> :- Japan and the southern part of Korea.

<u>pauciflora</u> :- From Kamtchatka, southwards through the islands of Japan, and is also found in the north of Korea.

<u>mannii</u> :- Only in the Cameroons and Fernando Po, on the west coast of Africa.

tristachya :- Only from Chile, in South America.

kobaysii :- Aleutians and St. Paul Island in the Bering Sea.

kjellmanniana :- Alaska, Kamtchatka, and part of Mongolia.

L. oahuensis occurs on the island of Oahu, in Hawaii, while *L. hawaiiensis* is found also on the other islands in the group. *L. longiflora* is found only on Lord Howe's Island, off the east coast of Australia. These three species are not strictly in the *campestris* complex, but are allied to it. They bear a considerable resemblance to each other, and to *crinita* and *banksiana*, both also species which occur only on islands. It seems possible that they have all arisen from a stock within the *campestris* complex, but the three former species, occurring on more isolated islands, have diverged farther from the original stock.

The chromosome number of several of the taxa in the complex is known. It is found that they fall into a polyploid series with a basic haploid number of 6.

If all the diploid taxa ($2n = 12$) have their geographical distributions drawn on one map, it is found that in only two cases do the areas occupied by them overlap. These cases are *echinata* and *bulbosa*, which overlap over the greater part of their range, and *campestris* and *pallescens*, which overlap over a relatively small part of their range. The areas occupied by these diploid taxa are, in general, far more restricted than those of the polyploid members of the series.

The tetraploid, hexaploid and octoploid taxa overlap far more with each other, and with the diploid taxa, as well as occupying rather wider areas.

The two cytological races (2n = 24 and 36) of *multiflora* have not been distinguished morphologically, neither have those of *congesta* (2n = 36 and 48). The number 2n = 16 appears to be anomalous, but, for reasons which will be given later, it is perhaps best treated as a diploid.

From the geographical distribution of the group, it would appear that it had arisen from the interaction of the diploid taxa, possibly by means of hybridisation and later polyploidy. The diploid members presumably had a common ancestor. The polyploid members of this group, as in others, have been able to spread beyond the boundaries occupied by their diploid ancestors.

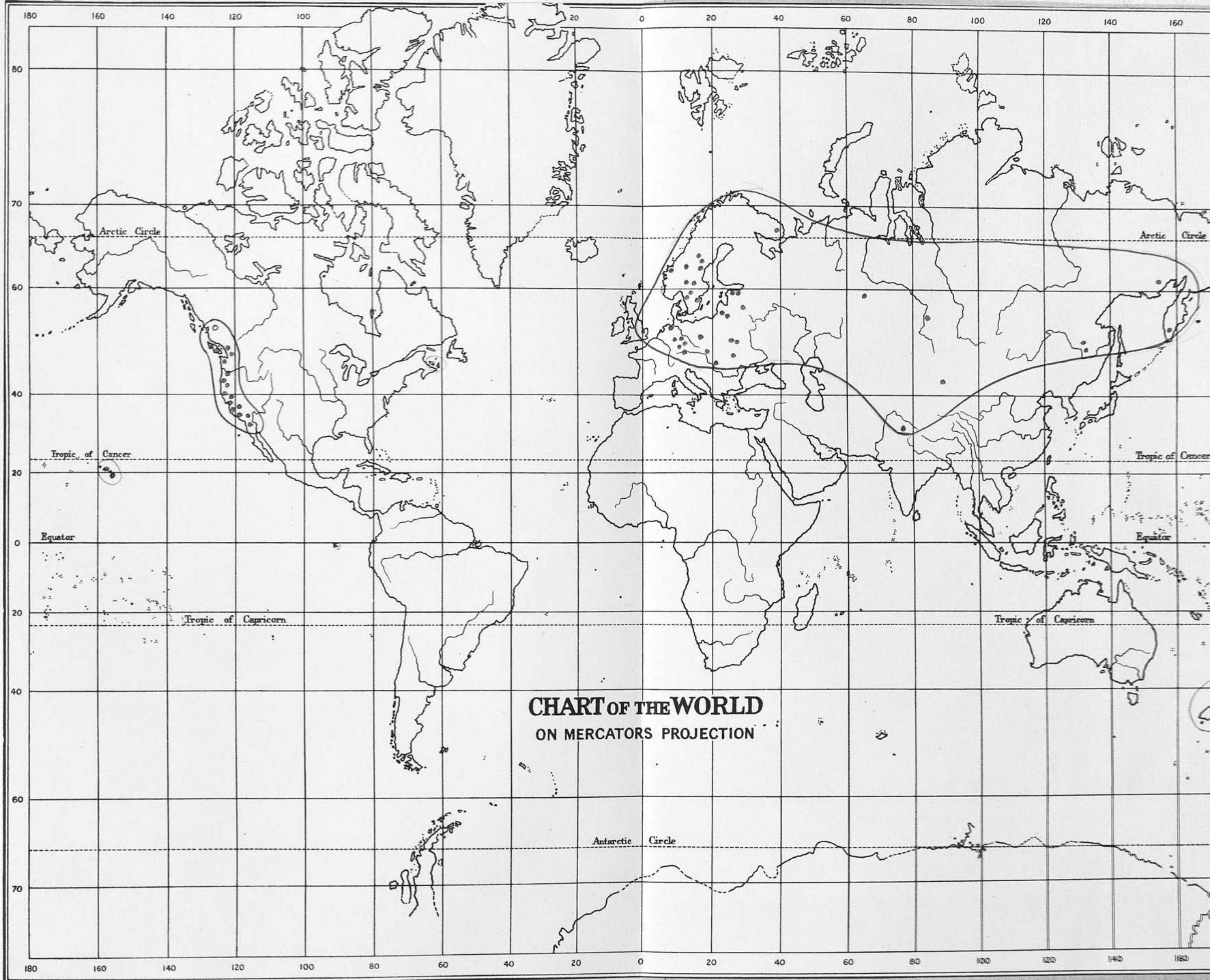

CHART OF THE WORLD
ON MERCATORS PROJECTION
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle

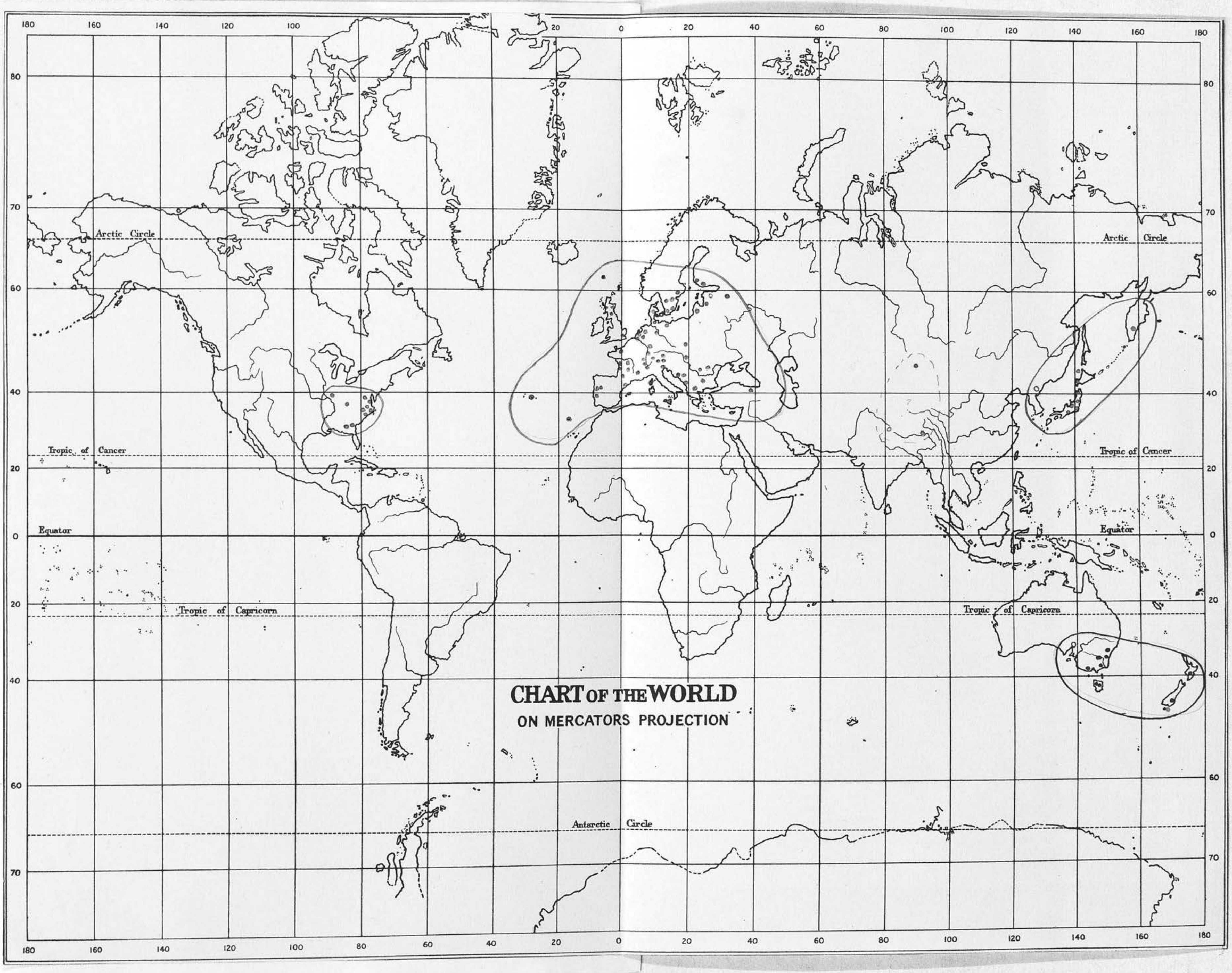

CHART OF THE WORLD
ON MERCATORS PROJECTION
Arctic Circle
Tropic of Cancer
Equator
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Antarctic Circle

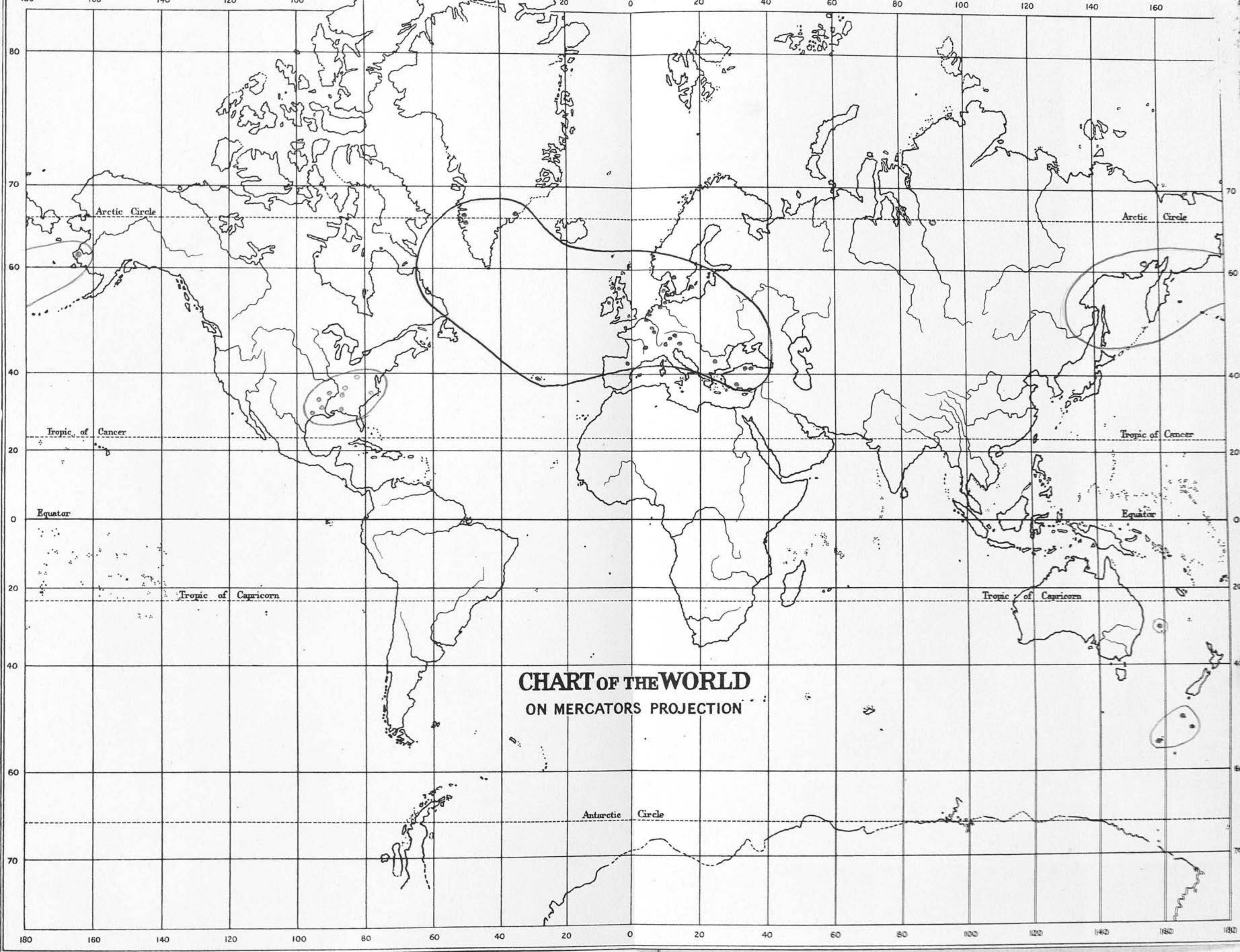
CHART OF THE WORLD
ON MERCATORS PROJECTION
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle
180
160
140
120
100
80
60
40
20
0
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60
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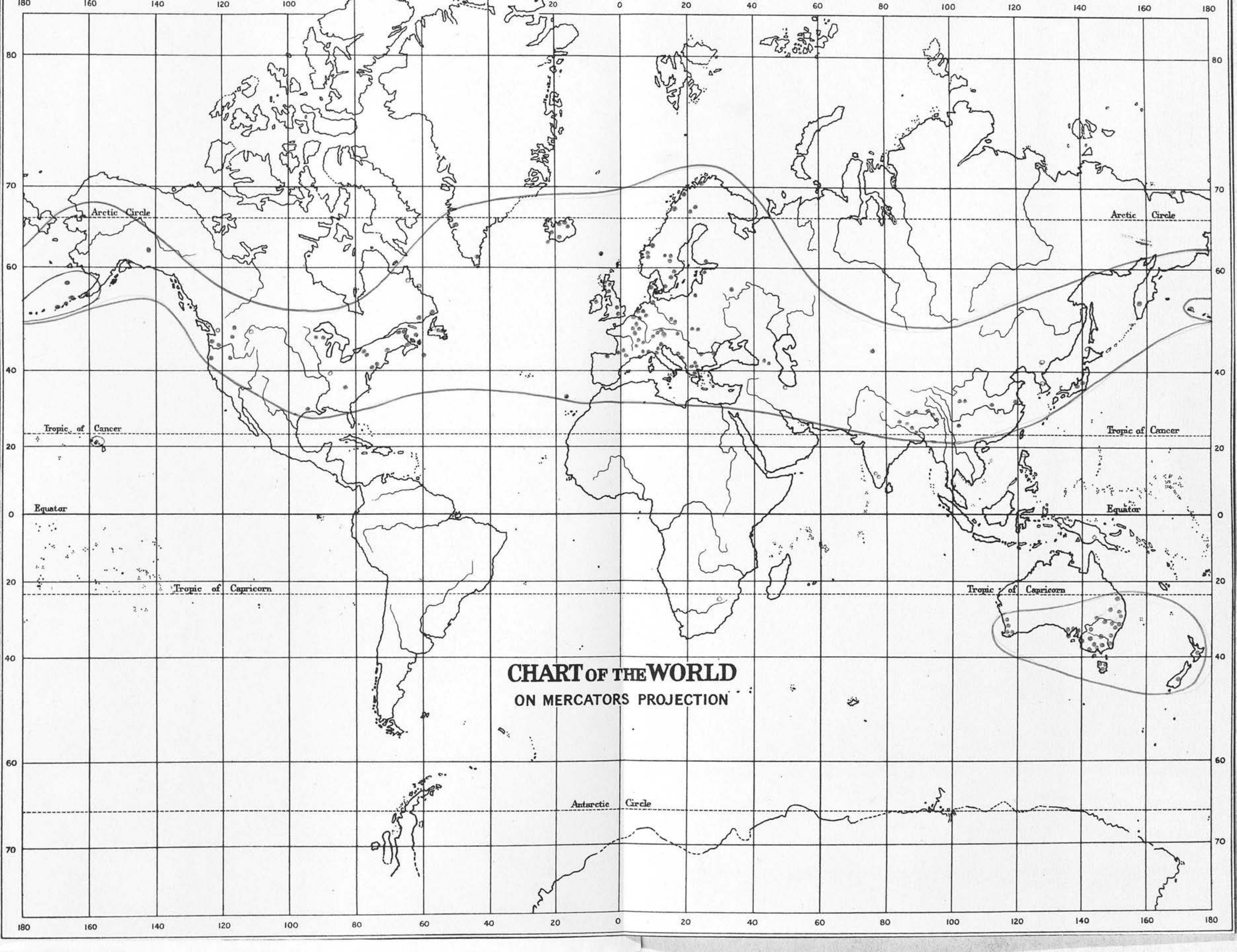

CHART OF THE WORLD
ON MERCATORS PROJECTION
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle

CHART OF THE WORLD
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Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle

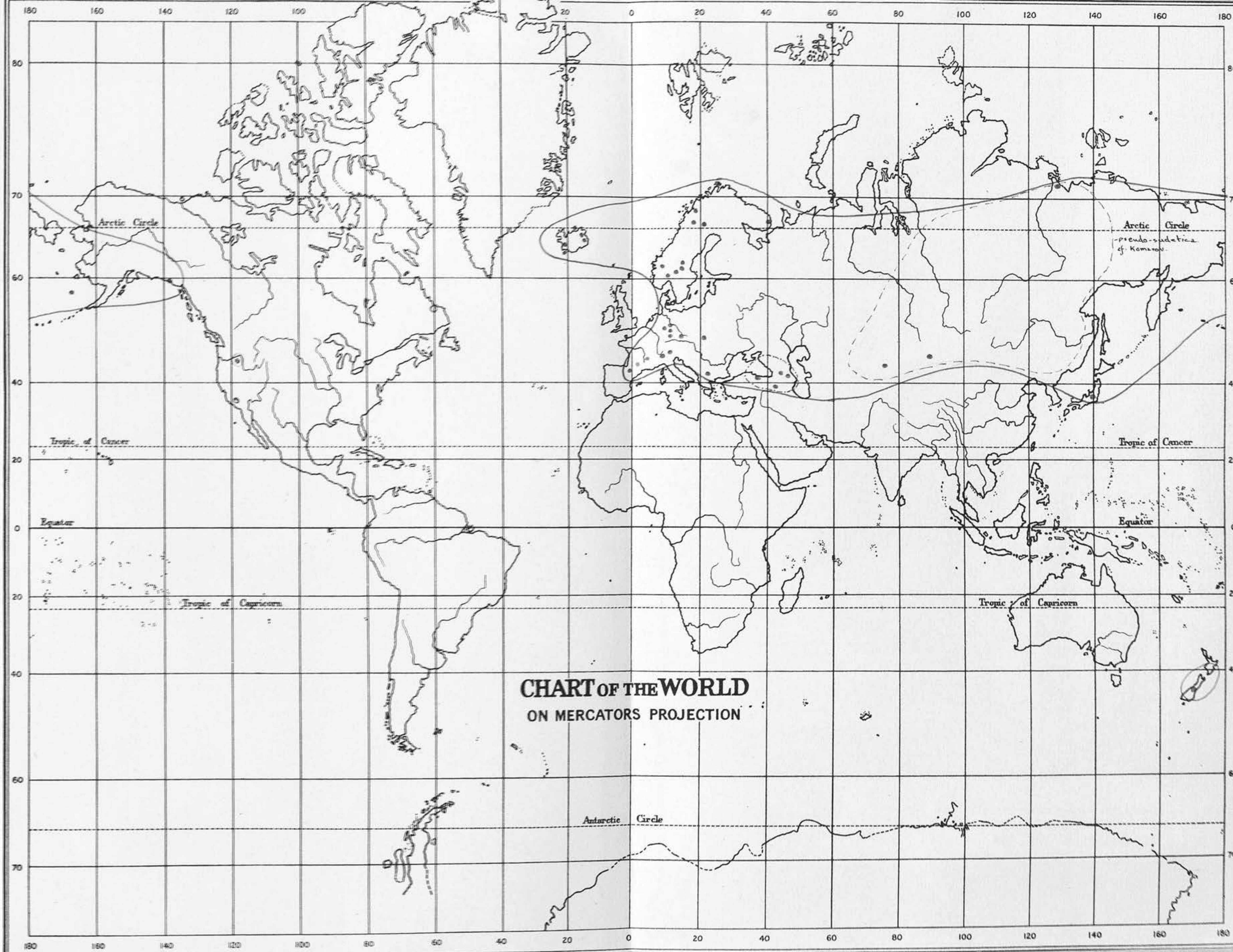
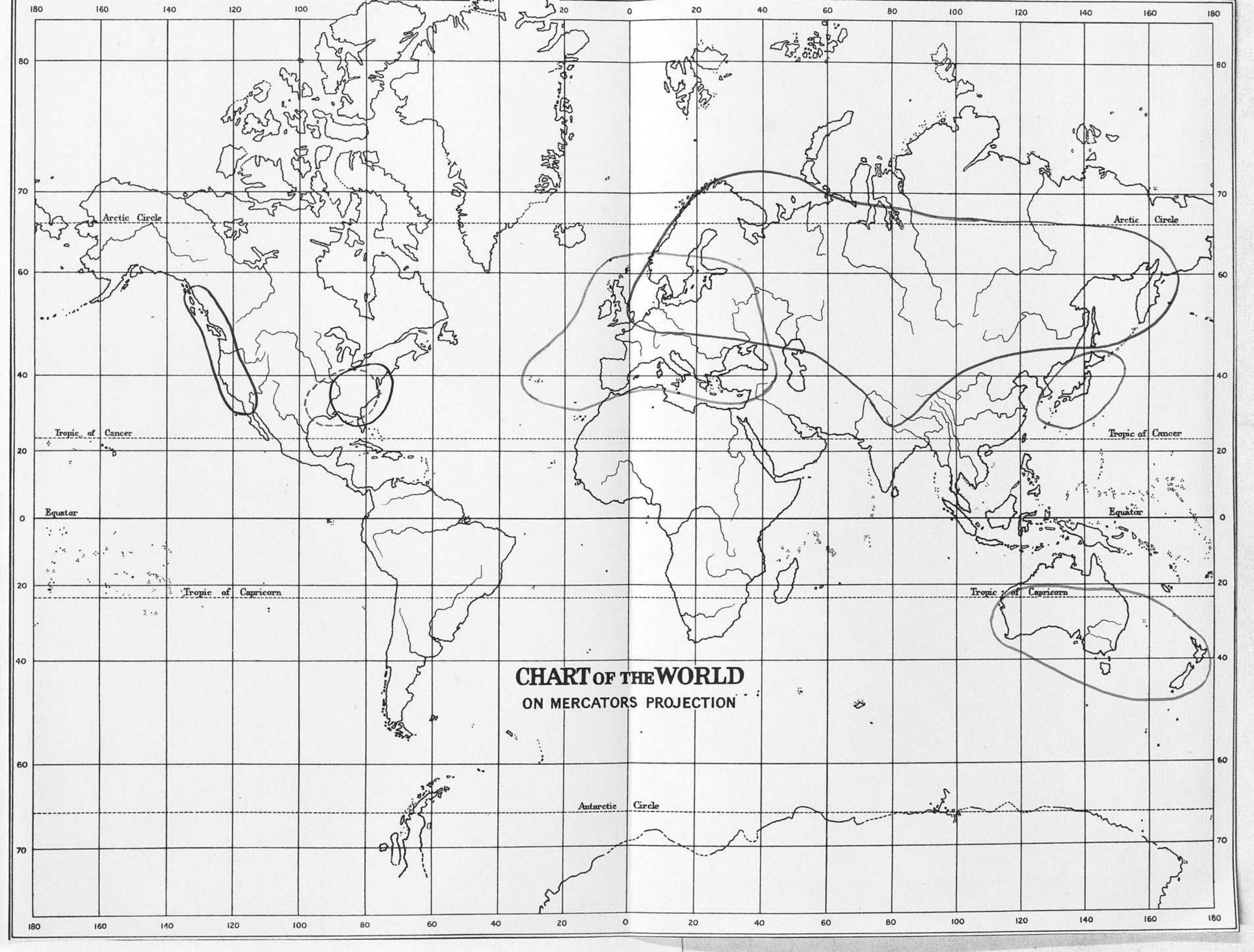


CHART OF THE WORLD
ON MERCATORS PROJECTION
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle
-pseudo-sudetica
cf. Komarov.



Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle
CHART OF THE WORLD
ON MERCATORS PROJECTION

III. GENERAL MORPHOLOGY.

A. INTRODUCTION.

A brief synopsis of the chief morphological characteristics of all the taxa in the complex was given in Chapter I. The European herbarium material was, however, studied in greater detail, the plants being measured in a manner similar to that used for the population analyses.

The characters used were as follows :-

Stem height (H) :- length from the base of the stem to the base of the inflorescence, measured in centimetres with a ruler.

Leaf length (L) :- length of leaf from node to tip (including both sheath and blade); the lowest cauline leaf was used in every case. Measured in centimetres and millimetres with a ruler.

Leaf width (B) :- the maximum breadth of the leaf blade. Measured in centimetres with calipers; accurate to 0.01 cm.

Number of flowers (F):- the total number of flowers in the inflorescence, estimated to the nearest 5; given in Roman numerals (e.g. I = 1-5, II = 6-10 etc.)

Number of heads (Sp) :- the total number of heads in the inflorescence.

Congestion Index (S) :- the mean length of the stalked heads in the inflorescence, measured in centimetres with calipers. The total length of the stalks (even if the heads appeared to be nearly sessile) was divided by Sp - 1, as the terminal head is always sessile.

Seed length : width (s/w) :- the ratio of the length of the seed (excluding the caruncle) to its width. Measured with an eyepiece micrometer in a microscope; measurements given in millimetres.

Seed size (s x w) :- an index of the size of the seeds, obtained by multiplying the length in mm. by the width in mm.; taken to two or three significant figures, after the elimination of decimals.

Stamen length (a + f) :- the length of the stamen (anther + filament) in millimetres. Measured with an eyepiece micrometer in a microscope.

Anther : total stamen ratio($\frac{a}{a + f}$) :- the relative size of the anther and whole stamen; a ratio of anther : filament would have resulted in some values of less than 1.0, and in others of more than 1.0, and would have necessitated the use of a logarithmic scale.

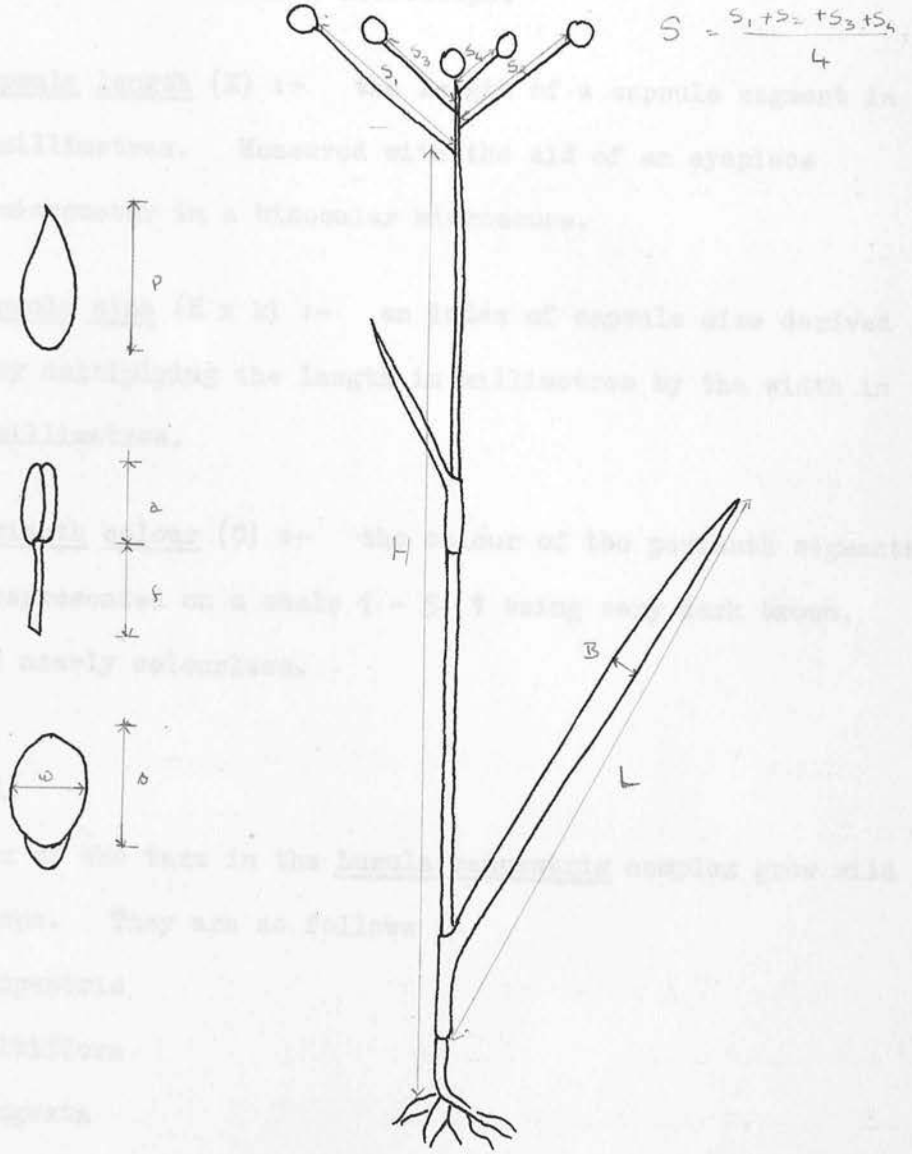


Fig. 9. Diagram of <u>Luzula</u> plant to show the measurements made.

Petal length (P) :- the length of an inner perianth segment; measured with the aid of an eyepiece micrometer in a binocular microscope.

Capsule length (K) :- the length of a capsule segment in millimetres. Measured with the aid of an eyepiece micrometer in a binocular microscope.

Capsule size (K x k) :- an index of capsule size derived by multiplying the length in millimetres by the width in millimetres.

Perianth colour (C) :- the colour of the perianth segments, represented on a scale 1 - 5, 1 being very dark brown, 5 nearly colourless.

B. EUROPE.

Six of the taxa in the Luzula campestris complex grow wild in Europe. They are as follows :-

campestris

multiflora

congesta

pallescens

sudetica

frigida

TABLE 1.

MAXIMUM, MEAN AND MINIMUM VALUES OF CHARACTERS FOR CONGESTA, MULTIFLORA, CAMPESTRIS, PALLESCENS, SUDETICA AND FRIGIDA.

	H cm.	L cm.	B cm.	F	Sp	S cm.	s/w	s x w	a + f mm.	$\frac{a}{a+f}$	P mm.	K mm.	K x k	C
congesta														
maximum	66.0	21.7	.63	XII	7	.64	1.87	177	2.00	.758	4.20	2.92	467	2
mean	30.0	10.0	.36	VI	4.5	.25	1.60	128	1.66	.543	3.38	2.67	414	
minimum	18.0	5.5	.18	III	2	.13	1.39	100	1.35	.409	2.67	2.54	353	
multiflora														
maximum	57.5	21.9	.56	XXII	19	2.71	1.84	152	2.25	.732	4.07	2.92	482	2 or 3
mean	27.0	10.42	.325	IX	6.3	1.28	1.59	105	1.73	.562	2.94	2.48	372	
minimum	11.5	5.0	.14	IV	3	.46	1.37	72	1.25	.417	1.80	1.80	207	
campestris														
maximum	23.5	12.3	.39	VIII	6	2.24	1.53	137	2.75	.882	4.32	3.17	565	1
mean	11.53	5.65	.237	V	3.5	1.06	1.36	105	2.03	.738	3.44	2.67	427	
minimum	3.0	2.3	.11	II	2	.17	1.20	98	1.40	.517	2.80	2.28	347	
pallescens														
maximum	29.5	17.2	.37	XIX	15	1.66	1.80	78	1.60	.579	2.67	2.41	290	4 or 5
mean	20.04	11.34	.246	IX	7.8	1.007	1.69	64	1.15	.489	2.04	1.95	224	
minimum	13.5	6.9	.18	IV	4	.59	1.62	48	.85	.369	1.78	1.78	181	
sudetica														
maximum	36.0	13.7	.46	XIII	11	1.95	1.73	107	1.50	.691	2.67	2.54	317	1
mean	21.66	8.53	.259	VI	4.4	..625	1.64	71	1.16	.498	2.00	1.91	214	
minimum	8.5	6.9	.11	III	1	.19	1.29	48	.85	.375	1.65	1.65	168	
frigida														
maximum	32.5	13.2	.42	IX	6	1.54	1.79	100	1.80	.566	3.30	2.80	355	1
mean	16.74	6.59	.246	V	3.6	.735	1.74	94	1.38	.503	2.60	2.41	295	
minimum	8.0	3.5	.13	I	1	.14	1.71	85	1.15	.375	2.28	1.80	229	

The herbarium material of these taxa available at the Royal Botanic Garden, Edinburgh, was measured in the manner described above, and a summary of these measurements is given in table 1.

The table includes the maximum, mean and minimum values for each character of each of the European taxa, and has been derived from measurements obtained from both British and European material in the herbarium.

Using these measurements as a standard for comparison, the specimens available in the herbaria at Kew and the British Museum were also examined, although this examination was less critical, as time did not allow the dissection and measurement of such a large amount of material. The majority of the plants in these herbaria did, however, fall into the six categories listed above. As with the Edinburgh material, a certain number of intermediate specimens occurred whose precise taxonomic position it was difficult to determine.

These intermediate specimens occurred particularly between _sudetica_ and _frigida_, and the examination of some gatherings of these groups from Scandinavia cast doubts on the status of the latter taxon. It does, however, seem to be distinct in most areas, and differs significantly from _sudetica_ in several respects, particularly in having considerably larger perianth segments, which are much longer than the ripe capsule.

There also appears to be a certain amount of confusion between frigida and multiflora in northern latitudes, possibly because the perianth of the latter becomes more intensely coloured in these regions, and also at higher altitudes. This is a feature which would require an experimental approach if it is to be satisfactorily investigated.

It seems possible that multiflora and pallescens hybridise on the Continent (and probably also in this country); a gathering from Czechoslovakia (Petrak 513) contains each of these taxa, together with some apparent intermediates.

To determine the nature of these intermedite forms, and to find out whether they are of hybrid or other origin, it would be necessary to study larger gatherings in more detail, in the same way as it has been possible to study the taxa occurring in Britain. In fact, experimental taxonomic studies of the group in different parts of Europe, e.g. the Alps, central Europe and Scandinavia, might be the only way of resolving these problems. They will, however, be reconsidered in the light of the detailed studies of the British taxa, and of the cytology of the whole group, which will be discussed in subsequent chapters.

It appears that campestris in the strict sense is fairly distinct in Europe, favouring similar situations to those which it occupies in Britain, particularly dry fields and pastures.

Multiflora grows in damper areas, often in woods, and appears, from the number of herbarium sheets, to be fairly common in Europe. By contrast, relatively few sheets of congesta are to be found in the herbaria, a fact which would appear to indicate that this taxon is rather less common on the Continent than multiflora. In Britain, on the other hand, these two taxa seem to be equally abundant, and occur in the herbaria in approximately equal numbers with campestris.

C. BRITAIN.

In Britain there are four members of the Luzula campestris complex: pallescens, multiflora, congesta and campestris. Of these, the last three are common and widespread throughout the country, while pallescens is extremely rare and local, occurring as a native only in Woodwalton and Holme Fens in Huntingdonshire.

The rank of these taxa has been treated differently in the various British floras, and in the local floras.

Bentham and Hooker, in the "Handbook of the British Flora", consider campestris, multiflora and congesta all as the one species, and mention L.multiflora Lej. as having "the peduncles so shortened as to give the appearance of L.spicata"; this obviously refers, in fact, to congesta. Pallescens is mentioned in a separate paragraph in brackets, but is treated more or less as a species; it was presumably thought to be too rare to be treated more fully.

In Clapham, Tutin and Warburg's "Flora of the British Isles" three species are recognised : campestris, multiflora and pallescens. Congesta is treated as a variety of multiflora.

L. sudetica is mentioned by Spence in his "Flora Orcadiensis" as being common in the Orkneys. Along with congesta (conjesta) it is treated as a variety of multiflora. Examination of herbarium specimens from Orkney does not substantiate the occurrence of sudetica in this region, and it seems likely that it was a dark-flowered form of multiflora which was observed. It is, however, possible that the range of sudetica might extend to Orkney and Shetland.

Examination of the herbarium material of campestris, multiflora and congesta shows that these form three groups, but that campestris is more distinct from the other two than the latter are from each other, Intermediate forms do occur, but not in such large numbers as to indicate widespread hybridisation, or the complete gradation of one taxon into the others. It is seldon impossible to assign a given specimen to one or other of the groups. More detailed examination of a larger number of individuals shows that there is a clear, but not complete gap between these taxa, and again demonstrates the slightly closer affinity of multiflora and congesta. The results of this detailed examination will be described in the chapter on Population Analyses, where they will be treated by statistical methods.

IV. ECOLOGY.

A. Introduction.

In the floras it is generally stated that, in addition to being morphologically distinguishable, *campestris* and *multiflora* show a definite ecological separation. *Campestris* is described as a plant of rather dry fields and rough pastures: *multiflora* as growing in damper places on moors and in woods, as well as in damp flushes and along river banks. In the latter situations it may be almost in association with *campestris*. The closer study of the ecological preferences of *campestris*, *multiflora* and *congesta* upholds this distinction, and also indicates a slight difference in habitat of the two latter taxa - *multiflora* preferring shadier places than *congesta*.

Communities containing one or more of these taxa have been studied in numerous localities in Britain, mostly in Scotland. Two or three communities were investigated in most of the localities, to give some idea of the variation in local conditions.

A summary of the ecology of the communities studied, together with the locality (8-figure grid reference given where possible), altitude etc. of each, is given in appendix I. Additional communities were studied from which mass gatherings were not made; these are summarised at the end of the appendix.

For each of the communities a brief note was made of the general type of habitat, aspect etc. For the majority, a list of the species growing with a plant of Luzula in a 1-metre square was made, usually expressed in their relative frequencies on the scale abundant, (a = more than 30% cover), frequent, (f = 15 - 30%), occasional, (o = 5 - 15%), rare, (1 or 2 plants). In a few cases, particularly where two of the taxa were growing in close proximity, a quadrat analysis was carried out, using a ¼ m. (25 x 25 cms.) quadrat and estimating the species on the basis of presence only. One line transect was also made, along which all three taxa occurred. ~~Three~~ Two communities of pallescens in Huntingdonshire were also visited.

In addition to studying the plants in the field, samples from other populations were grown in experimental plots at the Royal Botanic Garden, Edinburgh. These plants were from localities other than those studied in the field, each population being represented by from 4 to 6 plants. There were growing 3 populations of campestris, 3 of multiflora, 3 of congesta and 3 in which there was a mixture of multiflora and congesta, and also some intermediates. The flowering time, resistance to drought, etc. of these plants were noted for the seasons 1956 and 1957.

B. FIELD ECOLOGY.

(i) General:- Species lists.

The data from field ecology can be divided into three parts:

quadrat analyses, line transect and species lists. Species lists were made for the majority of the communities studied, while readings were made from only one line transect.

In all, about 60 populations were studied, mass gatherings of plants being collected from 50 of them. Of these, the majority were of multiflora or congesta, or mixed populations of these two. The features separating campestris from the other two taxa are more pronounced, and it was therefore decided to concentrate on multiflora and congesta.

In order to compare the ecology of the three taxa, 10 populations of each have been selected from the available data. The communities used were those for which the fullest ecological information had been obtained, and which also contained the purest population of the taxon under consideration.

The results of these analyses are given in tables 2, 3 and 4. The occurrence of each associated species is given as the number of times it is found in the ten populations. Three histograms were then drawn to compare the frequencies of all species associated in 4 or more instances with any one of the three taxa (fig. 10).

Several species were found in association with all three taxa, but on the whole there was a greater degree of similarity between the associates of multiflora and congesta, than there was between either of these and campestris. Festuca ovina and F. rubra, both plants which prefer a rather open and dry habitat, have frequencies

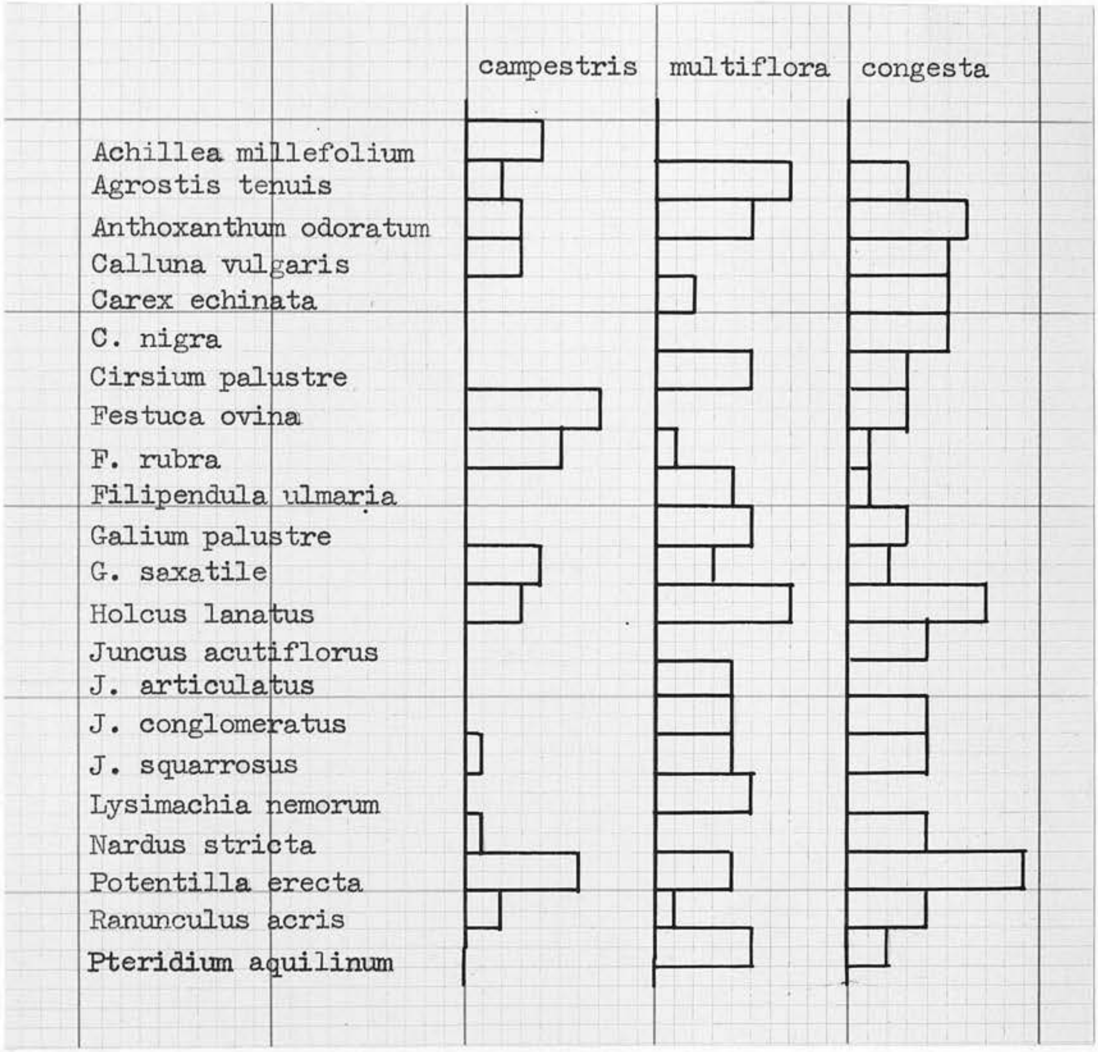


Fig. 10. Histogram of the relative frequencies of the species most often associated with campestris, multiflora and congesta.

TABLE 2.

SPECIES ASSOCIATED WITH LUZULA CAMPESTRIS IN A 1-METRE SQUARE.

	II C	VIII A	VIII B	IX A	IX B	IX C	X A	XI A	XII B	XXIII C	
Achillea millefolium	-	f	o	-	-	-	o	-	-	θ	4
Agrostis tenuis	+	-	-	-	-	-	-	-	-	a	2
Alchemilla alpina	+	-	-	-	-	-	-	-	-	-	1
Anthoxanthum odoratum	+	-	-	-	-	-	-	-	o	f	3
Bellis perennis	-	o	-	-	-	-	-	f	-	-	2
Calluna vulgaris	-	-	-	-	o	-	-	-	r	r	3
Campanula rotundifolia	+	-	-	o	-	-	-	-	-	o	3
Cardamine pratensis	-	-	-	-	-	-	-	r	-	-	1
Carex arenaria	-	-	-	-	-	-	-	f	-	-	1
C. panicea	+	-	-	-	-	-	-	-	-	-	1
Cerastium vulgatum	-	-	-	-	-	-	-	-	r	-	1
Cirsium arvense	-	-	-	-	-	-	-	f	-	-	1
Dactylis glomerata	-	θ	r	-	-	-	-	-	-	-	2
Deschampsia flexuosa	-	-	-	-	-	-	-	-	-	f	1
Equisetum arvense	-	-	-	-	-	-	-	r	-	-	1
E. palustre	-	-	-	-	-	-	-	o	-	-	1
Festuca ovina	-	a	a	a	a	f	a	-	-	o	6
F. ovina var. vivipara	-	-	-	-	-	-	-	-	a	-	1
F. rubra	-	a	f	-	f	f	-	a	-	-	5
Galium saxatile	-	-	-	-	o	f	-	-	f	f	4
G. verum	-	r	-	-	-	-	-	r	-	-	2
Holcus lanatus	+	-	-	-	-	o	-	-	r	-	3
Hydrocotyle vulgaris	-	-	-	-	-	-	-	o	-	-	1
Juncus squarrosus	-	-	-	-	-	-	-	-	f	-	1
Lotus corniculatus	-	o	o	-	-	-	-	-	-	-	2
Nardus stricta	-	-	-	-	-	-	o	-	-	-	1
Orchis incarnata	-	-	-	-	-	-	-	r	-	-	1
Oxalis acetosella	-	-	-	-	-	o	-	-	-	-	1

TABLE 2 (continued)

	II C	VIII A	VIII B	IX A	IX B	IX C	X A	XI A	XII B	XXIII C	
Parnassia palustris	-	-	-	-	-	-	-	o	-	-	1
Plantago lanceolata	-	o	f	o	-	-	-	-	-	-	3
Poa annua	-	f	-	-	-	-	-	-	-	-	1
P. pratensis	-	-	-	f	f	-	-	-	-	-	2
Polygala vulgaris	-	-	-	-	-	-	-	-	o	-	1
Potentilla erecta	+	-	-	f	o	-	o	-	f	f	6
Prunella vulgaris	-	-	-	-	-	-	-	f	-	-	1
Ranunculus acris	-	f	f	-	-	-	-	-	-	-	2
R. repems	-	o	-	-	-	-	-	-	-	-	1
Rumex acetosa	-	-	-	-	-	o	-	-	-	r	2
R. acetosella	-	-	-	-	-	-	-	-	o	-	1
Sieglingia decumbens	-	-	-	-	-	-	-	-	-	o	1
Senecio jacobea	-	-	o	-	-	-	-	r	-	-	2
Succisa pratensis	+	r	o	-	-	-	-	-	-	-	3
Taraxacum officinalis agg.	-	f	o	-	-	-	-	-	-	-	2
Thymus drucei	-	-	-	f	-	-	f	-	-	-	2
Trifolium repens	-	-	-	f	-	-	-	o	f	-	3
Vaccinium myrtillus	-	-	-	-	o	-	o	-	-	o	3
Valerianella locusta	-	-	-	-	-	-	-	r	-	-	1
Veronica chamaedrys	-	-	-	o	-	-	-	-	-	o	2
V. officinalis	-	-	-	o	-	-	r	-	o	-	3
V. serpyllifolia	-	-	-	-	-	-	-	-	r	-	1

TABLE 3.

SPECIES ASSOCIATED WITH <u>LUZULA MULTIFLORA</u> IN A 1-METRE SQUARE

	II A	III A	III B	III C	V A	V D	XIV A	XIV B	XIV C	XX II	
Agrostis tenuis	-	-	+	+	+	+	f	a	a	a	7
Ajuga reptans	-	f	-	-	-	-	-	-	-	-	1
Angelica sylvestris	-	-	-	-	-	-	-	-	-	o	1
Anthoxanthum odoratum	-	-	+	+	+	--	f	-	-	f	5
Bellis perennis	+	-	-	-	-	-	f	-	-	-	2
Betula sp. (seedling)	-	-	-	-	+	-	-	-	-	-	1
Blechnum spicant	-	-	-	-	-	-	f	-	-	-	1
Cardamine flexuosa	-	r	-	-	-	-	-	-	-	-	1
Carex echinata	-	r	-	-	-	-	o	-	-	-	2
C. panicea	-	-	-	-	-	+	o	-	-	-	2
C. remota	-	a	-	-	-	-	-	-	-	-	1
Carex spp.	-	-	+	+	-	-	-	-	-	-	2
Cerastium vulgatum	-	-	+	+	-	-	-	-	o	-	3
Chamaenerion angustifolium	-	-	-	-	-	-	-	-	-	o	1
Circaea intermedia	-	-	+	-	-	+	-	-	-	-	2
Cirsium palustre	-	a	-	+	-	+	o	o	o	-	5
Crataegus monogyna (seedling)	-	-	-	-	-	-	-	-	-	r	1
Crepis capillaris	-	f	-	-	-	-	-	-	-	-	1
Deschampsia caespitosa	-	-	-	-	-	-	-	-	-	f	1
D. flexuosa	-	-	-	-	-	-	a	-	-	-	1
Digitalis purpurea	-	-	-	-	-	-	-	f	-	-	1
Dryppteris filix-mas	-	-	-	-	-	-	-	o	-	-	1
D. spinulosa	-	r	-	-	-	-	-	-	-	-	1
Endymion non-scriptus	-	-	-	-	-	-	-	r	-	-	1
Epilobium montanum	-	-	-	+	-	-	-	-	-	-	1
E. palustre	-	o	-	-	-	-	-	-	o	-	2
Erica cinerea	-	-	-	-	-	-	o	-	-	-	1

Table 3 (continued)

	II A	III A	III B	III C	V A	V D	XIV A	XIV B	XIV C	XXII	
Festuca rubra	-	-	-	-	+	-	-	-	-	-	1
Filipendula ulmaria	-	f	+	+	-	+	[illegible]	-	-	-	4
Fragaria vesca	+	-	-	-	-	-	-	-	-	-	1
Galium saxatile	-	-	-	-	+	-	-	o	-	o	3
G. palustre	-	o	+	+	-	+	-	-	o	-	5
Geum urbanum	+	-	+	-	-	-	-	-	-	-	2
Glyceria fluitans	-	-	-	+	-	-	-	-	-	-	1
Holcus lanatus	-	-	+	+	+	-	f	o	f	o	7
Hypericum pulchrum	+	-	-	-	-	-	f	-	-	-	2
Juncus articulatus	-	a	+	+	-	-	-	-	o	-	4
J. bulbosus	-	-	a	-	-	-	o	-	-	-	2
J. conglomeratus	-	r	+	+	-	+	-	-	-	-	4
J. effusus	-	f	-	-	-	-	f	-	~~f~~	-	3
Lonicera periclymenum	-	-	-	-	-	-	-	-	-	o	1
Luzula pilosa	-	-	-	-	-	-	r	-	-	-	1
L. sylvatica	-	-	-	-	-	-	o	-	-	-	1
Lysimachia nemorum	+	f	+	-	-	+	-	o	-	-	5
Molinia caerulea	-	o	-	-	+	-	-	-	-	-	2
Orchis ericetorum	-	r	-	-	-	+	-	-	-	-	2
Poa memoralis	+	-	-	-	-	-	-	-	-	-	1
P. trivialis	-	f	-	-	-	-	-	-	-	-	1
Polygala serpyllifolia	-	-	-	-	-	-	o	-	-	-	1
Potentilla erecta	-	r	-	-	+	-	-	o	-	f	4
Primula vulgaris	-	-	+	+	-	-	-	-	-	-	2
Prunella vulgaris	+	f	-	-	-	-	-	-	o	-	3
Pteridium aquilinum	+	-	+	-	+	+	f	-	-	-	5
Ranunculus acris	-	-	-	~~+~~	-	-	-	-	-	-	1

Table 3 (concluded)

	II A	III A	III B	III C	V A	V B	XIV A	XIV B	XIV C	XXII	
Ranunculus flammula	-	f	-	-	-	+	-	-	f	-	3
R. repens	-	a	-	-	-	-	-	f	-	-	2
Rubus fruticosus agg.	-	-	-	-	-	-	o	-	-	-	1
Rumex acetosa	-	-	-	-	-	-	-	-	o	-	1
R.acetosella	-	-	-	-	-	-	-	o	-	-	1
Sagina procumbens	-	-	-	-	-	-	-	o	o	-	2
Salix sp.	-	-	-	-	+	-	-	-	-	-	1
Sanicula europea	-	-	-	-	-	-	o	-	-	-	1
Senecio jacobea	-	-	-	-	-	-	-	r	-	-	1
Sieglingia decumbens	-	-	-	-	+	-	o	-	-	-	2
Solidago virgaurea	-	-	-	-	-	-	o	-	-	-	1
Stellaria alsine	-	r	-	+	-	-	-	-	-	-	2
Succisa pratensis	+	-	-	-	-	-	-	-	-	o	2
Taraxacum paludosum	-	r	-	-	-	-	-	-	-	-	1
Teucrium scorodonia	-	-	-	-	-	-	f	-	-	-	1
Trifolium repens	-	-	-	-	-	-	-	-	-	o	1
Valeriana officinalis	-	-	-	+	-	-	-	-	-	-	1
Veronica chamaedrys	+	-	-	-	-	-	-	-	-	-	1
V. officinalis	-	-	-	-	+	-	-	f	-	-	2
V. serpyllifolia	-	-	-	-	-	-	-	r	r	-	2
Viola palustris	-	-	-	-	+	-	-	-	-	r	2
V. riviniana	-	o	-	-	-	-	-	-	-	-	1

Note : The species list from III A was made from a considerably larger area than those for the other populations; it consequently contains a relatively large number of species.

TABLE 4

SPECIES ASSOCIATED WITH LUZULA CONGESTA IN A 1-METRE SQUARE

	II B	IV A	IV B	IV C	V B	XII A	XIII B	XIII C	XV	XXIII A	
Achillea ptarmica	-	-	-	-	-	-	-	-	-	o	1
Agrostis stolonifera	-	-	-	-	-	-	-	+	-	-	1
A. tenuis	-	+	-	+	-	-	-	-	a	-	3
Alchemilla vulgaris agg.	-	-	+	-	-	-	-	-	-	-	1
Anthoxanthum odoratum	+	+	+	+	-	-	-	-	f	f	6
Betula pubescens	-	-	-	-	-	-	-	+	-	-	1
Blechnum spicant	-	+	-	-	-	-	-	-	-	-	1
Calluna vulgaris	-	+	-	+	-	o	-	+	f	-	5
Carex echinata	+	+	+	-	-	-	f	+	-	-	5
C. nigra	-	-	+	+	+	-	o	+	-	-	5
C. pulicaris	-	+	+	-	-	-	o	-	-	-	3
Cerastium vulgatum	-	-	-	+	-	-	-	-	-	-	1
Cirsium palustre	-	-	+	-	+	-	-	-	-	f	3
Crepis capillaris	-	-	-	-	-	-	-	-	o	-	1
Cynosurus cristatus	-	-	+	-	-	-	f	-	-	-	2
Deschampsia caespitosa	-	-	-	-	-	-	-	-	-	o	1
Empetrum nigrum	-	+	-	-	-	-	-	-	-	-	1
Epilobium palustre	-	-	-	-	+	-	-	-	-	r	2
Erica cinerea	-	+	-	-	-	-	-	+	-	-	2
E. tetralix	+	-	-	+	-	-	-	+	-	-	3
Eriophorum vaginatum	+	-	-	-	-	-	-	-	-	-	1
Festuca ovina	-	+	-	+	-	o	-	-	-	-	3
F. rubra	-	-	-	-	-	-	-	+	-	-	1
Filipendula ulmaria	-	-	-	-	+	-	-	-	-	-	1
Galium saxatile	-	-	-	+	-	f	-	-	-	-	2
G. palustre	-	-	f	-	-	-	f	-	-	o	3

Table 4 (continued)

	II B	IV A	IV B	IV C	V B	XII A	XIII B	XIII C	XV	XXIII A	
Holcus lanatus	+	+	+	-	+	r	o	-	-	o	7
Hydrocotyle vulgaris	-	-	-	-	-	-	f	-	-	-	1
Juncus acutiflorus	+	-	+	-	+	-	-	-	-	a	4
J. bulbosus	-	+	+	-	-	-	-	-	-	-	2
J. conglomeratus	-	-	+	-	+	-	-	+	-	o	4
J. effusus	+	-	-	-	-	-	f	-	o	-	3
J. squarrosus	+	-	+	+	-	f	-	-	-	-	4
Lathyrus pratensis	-	-	-	-	+	-	-	-	-	-	1
Leontodon autumnalis	-	+	-	-	-	-	-	-	-	-	1
Lolium peremne	-	-	-	-	-	r	-	-	-	-	1
Lotus corniculatus	-	-	-	-	-	-	-	-	o	-	1
L. uliginosus	-	-	-	-	+	-	-	-	-	-	1
Lychnis flos-cuculi	-	-	-	-	+	-	-	-	-	-	1
Mentha aquatica	-	-	-	-	-	-	o	-	-	-	1
Molinia caerulea	-	-	-	+	-	-	-	-	-	f	2
Myrica gale	-	-	-	-	-	-	-	+	-	-	1
Nardus stricta	+	+	-	+	-	a	-	-	-	-	4
Orchis maculata agg.	-	-	-	-	+	-	-	+	-	-	2
Parnassia palustris	-	-	-	-	-	-	-	-	-	r	1
Pedicularis palustris	-	-	-	-	-	-	o	-	r	-	2
Plantago lanceolata	-	+	+	-	-	-	-	-	-	-	2
Polygala vulgaris	-	-	-	+	-	r	-	-	-	-	2
Potentilla erecta	+	+	+	+	+	f	~~a~~	+	f	f	9
Prunella vulgaris	-	-	+	-	+	o	~~a~~	-	-	-	3
Pteridium aquilinum	-	+	-	-	-	-	-	-	r	-	2
Ranunculus acris	-	+	+	-	+	-	-	-	-	o	4
R. flammula	-	-	-	-	-	-	a	-	-	-	1

Table 4 (concluded)

	II B	IV A	IV B	IV C	V B	XII A	XIII B	XIII C	XV	XXIII A	
Salix aurita	-	+	-	-	-	-	-	-	-	-	1
Saxifraga aizoides	-	-	+	-	-	-	-	-	-	-	1
Stellaria alsine	-	-	-	-	+	-	-	-	-	-	1
Succisa pratensis	-	-	-	-	-	-	-	-	o	-	1
Thymus drucei	-	-	-	-	-	o	-	-	-	-	1
Trichophorum caespitosum	-	+	-	+	-	-	f	-	-	-	3
Trifolium repens	-	-	-	-	-	-	o	-	o	-	2
Ulex europaeus	-	-	-	-	-	-	-	-	r	-	1
Vaccinium myrtillus	-	+	-	-	-	-	-	-	-	-	1

of 70% and 50% respectively for campestris, 0 and 10% for multiflora and 30% and 10% for congesta. On the other hand, Holcus lanatus, a grass with a more distinct preference for shade and moisture, has a frequency of 30% for campestris, 70% for multiflora and 90% for congesta. The only species of Juncus occurring with campestris is J. squarrosus, and then only in one population, while 8 of the 10 populations of multiflora, and all those of congesta, had at least one species of Juncus growing with them.

Potentilla erecta was a frequent associate of each taxon, but was most abundant with congesta, where it occurred in 90% of the populations. Galium palustre was found with congesta and multiflora, but not with campestris.

A comparison of the species associated with congesta and multiflora shows several differences, which are perhaps less convincing than those mentioned above, but are, nevertheless, significant. It is observed that Calluna vulgaris occurred in 50% of the populations of congesta, but in none of the populations of multiflora, while Potentilla erecta was found in 90% and 40% of cases respectively; these are both predominantly moorland plants.

Species found more often with multiflora than with congesta include Lysimachia nemorum (in 50% with multiflora and not at all with congesta), Pteridium aquilinum (50% and 20%) and Agrostis tenuis (70% and 30%). The first of these is a typical woodland plant, and the Pteridium may itself provide some of the shade which multiflora appears to prefer, while Agrostis tenuis is a plant of grassland rather than of heather moors and bogs, but may be found in woods as well. Of the Juncus species, J. acutiflorus, a rush which grows in bogs and very wet places, occurs in 40% of the populations of congesta, but in none of those of multiflora; on the other hand, J. articulatus, which prefers damp, grazed meadows and moors, is found in 40% of the populations of multiflora, but not with congesta.

From a comparison of these populations it may be concluded that, in general, campestris prefers a considerably drier habitat than the other two taxa, being found in rough grazing land and similar situations. Congesta appears to grow most frequently in bogs and open moors, often in very damp places, while multiflora is generally found in woods, or in other situations where there is a certain amount of shade, but where the soil is also fairly moist. In areas where the trees have been felled in the not very distant past, multiflora may be found growing in the open, in which case its stature may be somewhat reduced; in these situations, also, a mixture of congesta and multiflora is a frequent occurrence.

(ii) Quadrat Analyses.

In two localities near Fortingal populations of campestris were found growing contiguously with congesta or multiflora. These were studied in greater detail ecologically, in order to determine whether or not a gradation in habitat resulted in hybridisation of campestris with either or both of the other taxa.

The populations investigated in this way were numbers I A, B and C, and II F (i), (ii), (iii) and (iv).

A quarter-metre quadrat (25 x 25 cm.) was used; 25 quadrats were sampled in each population, every quadrat containing a plant of Luzula. Each species present in the quadrat was noted, but no attempt was made to estimate relative abundance within the quadrat. The percentage frequency in 25 quadrats of each of the associated species was then calculated, and the percentages from different populations compared.

The results are given in table 5.

Populations I A, B and C.

The populations of group I were situated in a field just above the farm of Croftgarrow, near Fortingal, at an altitude of about 500 ft. The field was rough pasture, grazed by sheep and cattle. The ground sloped towards the east, being rather drier towards the top of the slope, and cut by several damp flushes, which are small streams in wet weather. Population A was situated on a rocky knoll at the top of the slope, where the soil was relatively dry - this population consisted mainly of campestris. Population B was from damper ground below A, while C was taken from a damp flush running alongside A and B. The two latter populations consisted largely of congesta, with some multiflora. The soil in the case of B was apparently intermediate in moisture content between that of A and C.

A comparison of the percentage frequencies of some of the species associated with Luzula in these populations illustrates the way in which these three habitats differ.

Agrostis tenuis has a frequency of 100% in population A, falling to 32% in B and 0% in C; Euphrasia agg. has a frequency of 68% in A, 12% in B and 20% in C; Galium saxatile occurs in 40% of the quadrats in A, but not at all in B or C, and Trifolium repens in found in 44% of A, 8% of B and 4% of C. These plants all favour a rather dry habitat, and are typical of rough pasture land. In several of these species population B occupies a position intermediate between A and C, though the percentage frequency of any species in it is usually nearer to C than it is to A.

Anthoxanthum odoratum occurs abundantly in all three populations, but increases from 72% in A to 80% in B and 96% in C; Juncus acutiflorus does not occur in A, but has a frequency of 56% in B and of 88% in C; Molinia caerulea is found in 16% of the quadrats in A, 52% in B and 96% in C; Succisa pratensis is found in 32% of the quadrats in A, and in 84% of those of both B and C. The last three species are typical of damp morrland, while Anthoxanthum odoratum is a grass which is tolerant of a wide variety of habitats.

Species which are more abundant in B than in either A or C include Galium verum (0, 68% and 4% in A, B and C respectively), Nardus stricta (0, 76% and 12%) and Potentilla erecta (40%, 92% and 76%). These plants are frequently found in very poor, rather acid grassland, with a reasonable amount of water in the soil.

By comparing the species found growing with Luzula in these three populations, it may be seen that the populations show a gradation from a dry habitat to a considerably more moist one. If the taxa of Luzula under consideration are able to hybridise, then this graded type of habitat ought to provide suitable conditions. The results obtained from the analysis of morphological data obtained from the mass gatherings will be discussed in a later chapter.

Populations II F (i), (ii), (iii) and (iv).

The four populations in this group were sampled in broad belts across the junction between a bog dominated by Myrica gale (i) and rough pasture grazed by sheep (iv). The transition zone is a grassy bank, which was probably formed by a glacial river terrace (see Plate 1[illegible]).

The lowest terrace is very wet and boggy, even after the 5 or 6 weeks of drought which had preceded this investigation, and was dominated by Myrica gale, accompanied by abundant Juncus acutiflorus. This is followed by a zone dominated by Juncus acutiflorus at the foot of the slope (ii); the next zone is the slope itself (iii), covered by much taller grass, and with rather damper soil than the pasture above (iv). Luzula was found growing in all these zones, congesta in the bog and Juncus area and campestris in the pasture. The forms on the slope were intermediate in height and other vegetative characters which could be observed in the field, a feature which might be caused either by the intermediate nature of the habitat, or by hybridisation between the two taxa. (Fig. 11).

It seemed that this would be an ideal habitat for hydridisation to occur, if the plants are indeed able to do so, since there are two contiguous populations containing two different taxa of Luzula, with a gradation between their habitats, and an apparent gradation in the plants of Luzula themselves.

Approximately 25 plants of Luzula were collected from each of five broad bands parallel to the zones; the intermediate zone (iii) was split into two, and collections made at a lower level (a) and an upper level (b). The results of the analyses of the morphological characters of these plants will be discussed later.

The quarter-metre quadrat was again used for populations (ii), (iii) and (iv), but it was too small to use in population (i). In this case, Myrica gale and Juncus acutiflorus were very frequent, all other species occurring in the population being only occasional, so the species found in association with Luzula were merely listed without the use of a quadrat.

The only species occurring in all four zones are Potentilla erecta and Succisa pratensis; most of the other species tend to have their greatest frequency in either (i) and (ii) or in (iii) and (iv), although a few are most frequent in (ii) and (iii).

Potentilla erecta is most abundant in (iii), where it is found in 96% of the quadrats, and is also very frequent in (iv) (84%), and is found in 44% of (ii), and in (i); Succisa pratensis is also most frequent in (iii) (24%), falling off in (ii) (16%) and in (iv) (4%).

Molinia caerulea occurs only in (iii), where it has a frequency of 20%. Anemone nemorosa was found in 56% of the quadrats in (iii), and in 16% of those in (iv), while it did not occur at all in (i) and (ii). This part of the area was probably once wooded, as it still is both up- and down-stream from the locality, and the Anemone may be a relic of the woodland flora.

Myrica gale is the dominant plant in (ii), but it grows only in the wettest part of the bog, and this community is well defined. It is separated from the drier ground by a zone dominated by Juncus acutiflorus, a species which has a frequency of 100% in (ii) and is abundant in (i) but only occurs in 4% of the quadrats in (iii). Other plants which occur in either (i) or (ii), or both, but not in (iii) or (iv), include Epilobium palustre, Drosera rotundifolia, Viola palustris, Galium palustre and Cirsium palustre: all plants which favour a very wet habitat.

Plants which occur in (ii) only, or in (ii) and (iii), include Carex echinata (84% and 40% respectively), C. nigra (36% and 16%) and C. pulicaris (8% and 0). Ranunculus flammula is found in 12% of (ii) and in only 4% of (iii), and Achillea ptarmica in 8% and 4% respectively.

Species whose frequency is highest in (iii) and (iv) include the grasses Agrostis tenuis (44% and 40% respectively), Festuca rubra (76% and 96%) and Anthoxanthum odoratum which occurs in 40% of (ii), and in 76% of both (iii) and (iv); Prunella vulgaris similarly increases 24%, 24% and 44% from (ii) to (iv). These plants, particularly the grasses, are typical members of a rough pasture community.

A list of the Bryophytes found in association with the flowering plants in the area was also made. Sphagnum spp. was found in (i) and (ii), but not in the drier areas of (iii) and (iv), and Polytrichum commune only in (ii). Mnium punctatum and M. undulatum were found in (iii), as were Rytidiadelphus triquetrus and Pseudoscleropodium purum. Rytidiadelphus squarrosus was found in both (iii) and (iv), and is a moss which is usually found in situations which are reasonably well drained. Thuidium tamariscinum was found in (ii), (iii) and (iv). The bryophytes show a similar picture to that given by the flowering plants, but there are several species which are found (i) and (iii) but not in (ii) and (iv), or with a similar discontinuity.

If an analysis is made of the numbers of species occurring in only one community, in two, and in three, an idea of the general relationships of the communities to each other may be formed. The results of this analysis are given in the table below :-

Community.	Number of species.
in all 4	2
(i) only	3
(ii) only	10
(iii) only	4
(iv) only	9
(i) & (ii)	5
(ii) & (iii)	5
(iii) & (iv)	8
(i) (ii) & (iii)	1

Community	Number of species.
(ii) (iii) & (iv)	4
total in (i) & (ii)	18
total in (ii) & (iii)	13
total in (iii) & (iv)	21

It will be seen that there are 18 species which occur in (i) and (ii) together, but not in (iii) and (iv), while there are 21 which are found in (iii) and (iv) together but not in (i) and (ii). The number of species which are found in (ii) and (iii) but not in (i) or (iv) is only 13, which may indicate that (ii) and (iii) are less similar to each other than are (i) and (ii) or (iii) and (iv).

The evidence from this locality again shows that campestris, which is found in (iii) and (iv) favours a dry habitat, and that congesta, which is found in (i) and (ii), and also in (iii), is more a plant of wet boggy areas, though it can grow in the same habitat as campestris, if this is not too dry. A few plants of multiflora were found in (iii), a part of the area which may at one time have had more than the single Ash tree which is left.

(iii) Line Transect II E.

Only one line transect was made, in an area similar to that of II F, but with rather more shade. The locality was about 100 yards farther up Glen Lyon than II F, and the transect passed from open, dry pasture, through a shaded area on a slope to a more level, open, boggy situation at the foot of the slope. A diagram of the general profile of the area is given in fig. 12, with the position of the transect marked on it.

The species occurring along the transect were noted at intervals of one foot. Any plants of Luzula occurring along the transect, or within a foot on either side of it, were collected, and their position relative to each other noted. Subsequent examination of these plants showed that campestris, multiflora and congesta were all present.

At the beginning of the transect (fig. 13), the plant most frequently occurring is Festuca ovina, and, associated with it, Agrostis tenuis, Galium saxatile, Trifolium repens and Luzula campestris. In the central, shaded part, Anthoxanthum odoratum and Holcus mollis become more frequent, and also found are Oxalis acetosella, Anemone nemorosa, Endymion nonscriptus and a few Luzula plants, both campestris and multiflora. At the foot of the slope a zone with Juncus spp. is passed through (J.bulbosus, J.effusus, and J.acutiflorus) in which Ranunculus flammula, Holcus lanatus, Galium palustre and Luzula congesta also occur. There is only one plant of Myrica gale on the transect, but if this had been carried a few yards further, it would have extended into the area dominated by this species.

The three zones on the transect correspond roughly to (iv), (iii) and (i) and (ii) of locality II F. The central zone in the transect has retained the trees which were possibly once present in II F, but are now represented by a solitary Ash tree.

Examination of the Luzula plants collected along this transect show that the plants in the pasture at the top of the slope are campestris, which extends well down the slope and occurs in the shaded part. Also found in the shaded zone is multiflora, which is followed, in the Juncus zone, by congesta. There is some intermixing of the taxa, but the transect does show the preference of campestris for a dry habitat, of multiflora for a moister, shady one and of congesta for even damper soil, and a less shaded situation.

C. CONCLUSION.

From the evidence given above, it seems that the habitat preferences of campestris, multiflora and congesta in Britain, while not restricted, are reasonably distinct.

The preference of campestris for dry habitats is observed in most of the British floras, and that of multiflora and congesta for damper, more acid soils is noted by comparison. The ecological separation of multiflora and congesta in this country has not, however, been widely appreciated. That this separation does exist is demonstrated in the preceding pages, and, although it is far from being sufficiently complete to prevent inter-breeding, it must be the result of a significant physiological difference between these two taxa.

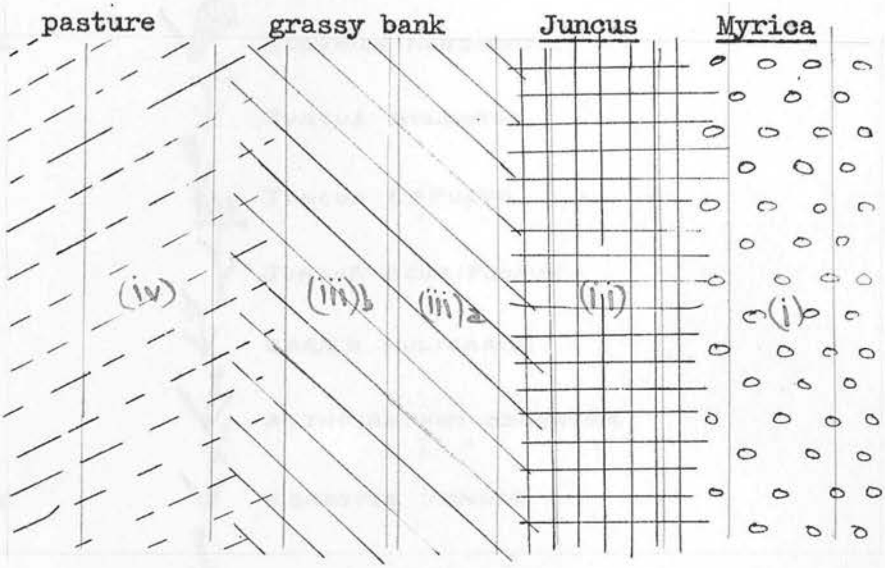


Fig. 11. Plan of the relationships of the habitats and areas sampled in II F.

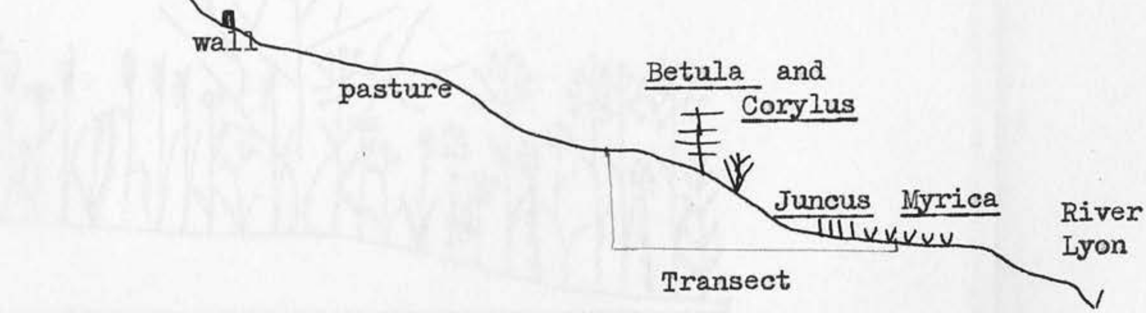


Fig. 12. Diagram of profile of hillside on which line transect II E was made.

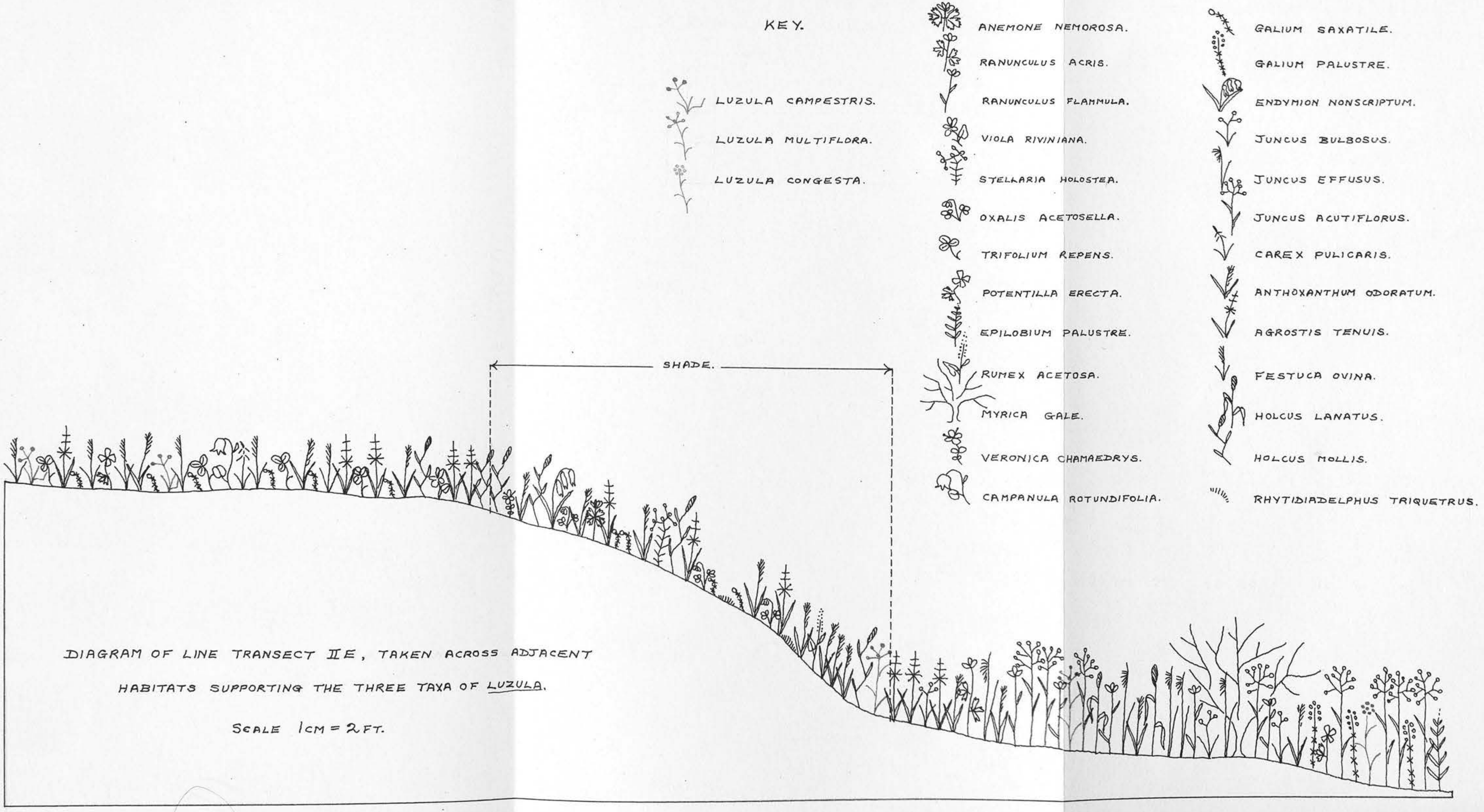


DIAGRAM OF LINE TRANSECT IIE, TAKEN ACROSS ADJACENT HABITATS SUPPORTING THE THREE TAXA OF <u>LUZULA</u>.

SCALE 1CM = 2FT.

FIG. 13

TABLE 5.

PERCENTAGE FREQUENCIES OF SPECIES ASSOCIATED WITH LUZULA IN TWENTY-FIVE 25 x 25 cm. QUADRATS

	I			II F			
	A	B	C	(i)	(ii)	(iii)	(iv)
Achillea millefolium	8	-	-	-	-	-	4
A. ptarmica	-	-	-	-	8	4	-
Agrostis tenuis	100	32	-	-	-	44	40
Anemone nemorosa	-	-	-	-	-	56	16
Anthoxanthum odoratum	72	80	96	-	40	76	76
Betula sp. (seedling)	-	-	-	-	-	-	4
Briza media	-	8	28	-	-	-	-
Calluna vulgaris	4	4	-	-	-	-	-
Campanula rotundifolia	-	-	-	-	-	-	40
Cardamine pratensis	-	-	-	-	8	-	-
Carex echinata	-	-	-	-	84	40	-
C. nigra	-	12	12	-	36	16	-
C. pulicaris	-	20	28	-	8	-	-
Carex spp.	12	-	8	-	16	-	-
Centaurea nigra	24	12	-	-	-	-	-
Cerastium vulgatum	8	-	-	-	-	-	12
Cirsium palustre	-	-	-	+	-	-	-
Cynosurus cristatus	-	20	20	-	-	-	-
Deschampsia flexuosa	-	-	-	-	-	4	4
Drosera rotundifolia	-	-	-	+	-	-	-
Epilobium palustre	-	-	-	+	40	-	-
Erica tetralix	-	-	-	+	-	-	-
Euphrasia agg.	68	12	20	-	4	-	-
Festuca rubra	-	-	-	-	-	76	96
Filipendula ulmaria	-	-	-	+	24	-	-
Fraxinus excelsior (seedling)	-	-	-	-	24	-	-

Table 5 (continued)

	I			II F			
	A	B	C	(i)	(ii)	(iii)	(iv)
Galium saxatile	40	-	-	-	4	88	92
G. palustre	-	-	-	-	20	-	-
G. verum	-	68	4	-	-	-	4
Gentianella campestris	8	-	-	-	-	-	-
Hieracium pilosella	-	4	-	-	-	-	-
Holcus lanatus	84	36	84	+	24	-	-
Juncus acutiflorus	-	56	88	a	100	4	-
J. bulbosus	-	-	-	-	4	8	-
J. effusus	-	-	-	-	8	-	-
Leontodon autumnale	8	8	-	-	24	-	-
Linum catharticum	-	-	8	-	-	-	-
Lotus corniculatus	16	36	8	-	-	4	-
Lychnis flos-cuculi	-	-	-	-	4	-	-
Lysimachia nemorum	-	-	-	-	8	-	-
Molinia caerulea	16	52	96	-	-	20	-
Myrica gale	-	-	-	d	4	-	-
Nardus stricta	-	76	12	-	-	-	-
Narthecium ossifragum	-	4	12	+	-	-	-
Orchis maculata agg.	-	4	-	-	-	4	-
Pinguicula vulgaris	-	-	4	-	-	-	-
Plantago lanceolata	48	56	56	-	-	12	28
Polygonum viviparum	-	-	-	-	-	-	4
Potentilla erecta	40	92	76	+	44	96	84
Prunella vulgaris	36	12	-	-	24	24	44
Pteridium aquilinum	28	-	-	-	-	-	-
Ranunculus acris	40	16	24	-	20	16	12
R. flammula	-	-	8	-	12	4	-
Rumex acetosa	-	-	-	-	-	-	12
R. acetosella	8	-	-	-	-	-	-

Table 5 (concluded)

	I			II F			
	A	B	C	(i)	(ii)	(iii)	(iv)
Sagina procumbens	-	-	-	-	-	-	4
Senecio jacobea	8	-	-	-	-	-	-
Sieglingia decumbens	-	-	-	-	-	4	16
Succisa pratensis	32	84	84	+	16	24	4
Trifolium pratense	-	32	24	-	-	-	-
T. repens	44	8	4	-	-	28	52
Veronica chamaedrys	-	-	-	-	-	-	44
V. officinalis	-	-	-	-	-	4	-
Viola palustris	-	-	-	+	32	-	-
V. riviniana	-	-	-	-	-	36	16
Bryophytes							
Calypogeia trichomanis				+	-	-	-
Lophocolea bidentata				+	+	-	+
Plagiochila asplenioides				-	-	-	+
Sphagnum sp.				+	+	-	-
Eurynchium sp.				+	-	+	-
Hylocomium splendens				-	+	+	-
Mnium longirostrum				-	+	-	+
M. punctatum				-	-	+	-
M. undulatum				-	-	+	-
Polytrichum commune				-	+	-	-
Pseudoscleropodium purum				-	-	+	-
Rytidiadelphus squarrosus				-	-	+	+
R. triquetrus				-	-	+	-
Thuidium tamariscinum				-	+	+	+

D. PERFORMANCE UNDER CULTIVATED CONDITIONS.

About 50 plants of Luzula were grown in the experimental plot at the Royal Botanic Garden, Edinburgh, for a period of about three years from 1955 until 1958. The times of flowering, and of setting seed of these plants was noted, and observations were made on their response to the conditions under which they were grown.

It was observed that campestris was the first group to start flowering, about the end of March: it continued to flower throughout April and May, and went on into June, though most of the seed was ripe by the end of June. Multiflora started to flower at the end of May, continuing through June and July; by the end of July most of the seed was ripe. The flowering time of congesta was approximately the same as that of multiflora, but was, on the average, a week or two later. (Fig. 14).

The overlap in flowering times of campestris and of multiflora and congesta is sufficient to allow some hybridisation to take place, so long as other conditions allow, but it is not of sufficient duration to permit interbreeding on a major scale. The flowering times of multiflora and congesta, on the other hand, offer no barrier to complete interbreeding.

These plants were all grown under the same conditions, in the open, in normal garden soil; their ability to adapt themselves to these conditions, which varied to a greater or lesser degree from those found in their natural environment. The soil was possibly best suited to campestris, as it was fairly dry; the plants belonging to this taxon grew well, forming dense cushions 8 or 10 inches across. The stolons usually associated with campestris did not develop to any great extent; they may possibly arise in response to competition from other plants in a closed community. The flowering stems in this taxon were generally rather longer than are usual in the field, which may be due to the absence of grazing. Plants of campestris found growing in the lawns at the Royal Botanic Garden flowered freely, but their stems were only 2 - 3 cm. high, owing to their being frequently cut along with the grass. These plants also developed stolons in the normal way, and a single plant often covered an area 1 or 2 feet across.

The plants of multiflora and congesta, on the other hand, tended to have stems rather shorter than those of plants collected in the field. The height of a plant in the field does, however, seem to depend to some extent on the plants with which it is associated, being taller if growing with tall plants. Both multiflora and congesta flowered and set seed normally in 1955, which was a warm, fairly dry summer. In 1956, however, there was a marked difference in the response of the two taxa to weather conditions. In that year, there was remarkably little rain during the spring, until the end of June. The plants of multiflora flowered and set seed normally, but congesta flowered very poorly and set hardly any seed. The drought was followed by a very wet spell, and not much of the seed which had set was ripened.

It would seem from this evidence that multiflora can withstand drought rather better than congesta, and this would indicate a slight physiological difference between the two taxa, a fact which is also indicated by the requirements of these plants in the field.

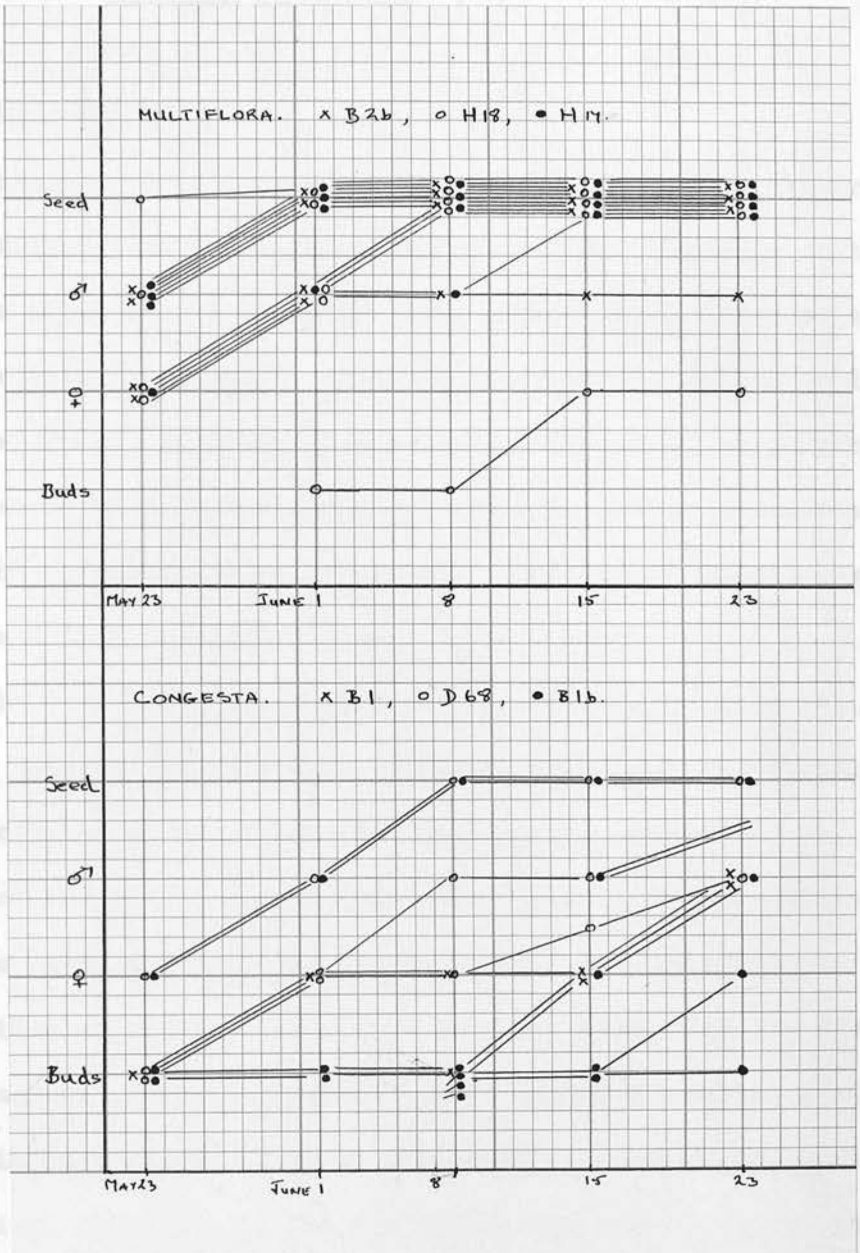


Fig. 14. Diagram of the times of flowering of the cultivated plants of <u>multiflora</u> and <u>congesta</u>.

V. DETAILED MORPHOLOGY (Population Studies).

A. INTRODUCTION.

Examination of herbarium material of Luzula from the British Isles showed that three major groups, or taxa, occurred, with one smaller group representing the rare pallescens. Intermediate plants were relatively frequent, although the majority of them could be assigned to one or other of the taxa. The number of herbarium specimens available for study was limited, and so, since the plants with the exception of pallescens are exceedingly common, mass gatherings were made from localities throughout Scotland.

The herbarium material is of limited use, in any case, since the plants had been collected at different stages of development, and it was necessary to have ripe seed in order to utilise all the characters in which the plants show differences. Also, it was observed from cultivated plants that the stem continued growing after the time of flowering, and went on until the seed was ripe, when the maximum height was reached. Thus, stem height could only be considered significant if an inflorescence had fully ripe seed. Accordingly, the mass gatherings were made in the field when the seed was ripe, that is, from mid-June for campestris and from mid-July for congesta and multiflora. Plants grown in the Royal Botanic Garden, Edinburgh were also collected at this time.

The characters used for the study of these mass gatherings were the same as those used for investigation of the herbarium material.

A total of 50 gatherings ~~were~~ was made, representing some 1500 plants. Several populations were collected from each area visited.

B. METHODS.

From 25 - 60 plants were collected from each population, depending on the frequency of Luzula in the community, and on the degree of variability which was apparent in the field. Thus, for a mixed population of congesta and multiflora 40 or 50 plants might be collected, while in a relatively pure population of any of the taxa the number collected would be only 25 or 30. This may have resulted in an abnormally high proportion of intermediate forms having been collected; the number of them occurring certainly seems to be relatively larger than it is among the herbarium specimens. On the other hand, the lack of intermediates in the herbaria might be due to selection by the collectors of only "typical" forms.

The method of collecting was to take one inflorescence from each plant. This was usually the tallest, to give some degree of consistency to the sampling method. The inflorescence was cut off right from the base, so that all the cauline leaves were present on the stem, and so that the maximum stem height could be measured.

The plants were pressed and then stored in newspapers until they could be measured in the laboratory later in the year. The measurements were made as described in chapter 3. A list of these measurements, together with the symbols used for the sake of convenience and brevity to represent them, is given below :-

Stem height	H
Leaf length	L
Leaf width	B
Number of heads per inflorescence	Sp
Number of flowers	F
Stamen length	a + f
Anther total stamen length	$\frac{a}{a + f}$
Seed length:width	s/w
Seed size	s x w
Perianth length	P
Congestion index	S

The "macro" characters, such as stem height, leaf length, etc. were measured first; from each plant one flower was removed at random, and from it one inner perianth segment, one stamen and one seed were taken. These were then mounted on a strip of "Sellotape" which had been placed adhesive side up on a microscope slide; all the stamens from any one population were kept on one slide, all the perianth segments on another and the seeds on a third. To make a more or less permanent mount of the two former, another slide was laid on top of the "sellotape", the original slide removed and the "sellotape" pressed well down so that as much air as possible was excluded, and the stamens and perianth segments were adhering closely to the slide. The seeds were too thick for this method to be used, so another slide was merely laid on top of the seeds, and the two slides were bound together at the ends.

The seeds, stamens and perianth segments were than all measured at the same time, using a microscope with an eyepiece micrometer. The readings were later converted to millimeters.

Each plant in every population was numbered with a small tie-on label, so that any individual plant could be located later on, if it should prove necessary to check measurements already made, or to make a new set of measurements of a character not previously investigated. The seeds, stamens and perianth segments were also numbered on the slides, so that they could be referred to the plants from which they came.

The ratios seed length:width and anther : total stamen length were calculated from the measurements with the aid of a slide rule.

C. VARIATION IN INDIVIDUAL CHARACTERS.

When all four British taxa are examined, each character shows a considerable range of variation. The ranges of variation of the different taxa cover part of the total range, and they may or may not show a certain amount of overlap. The variation of each taxon in the different characters will be discussed below. The information was obtained from the mass gatherings, which included large numbers of plants of multiflora, congesta and campestris, but, because of its rarity, only a few plants of pallescens. This last taxon, has, however, been included in the account, so that it can be compared with the other three, although the range of variation given for it must be considerably less than the actual range.

1. Stem Height.

These was a total range in stem height of from 4.0 to 74.5 cms. If these measurements are made into a frequency histogram, it is found that this is very markedly skewed towards the lower end of the scale, with the mode at about 30 cms. An attempt to produce a closer approximation to a normal distribution from these data was made by converting them into logarithms. This, however, had the effect of skewing the curve towards the other end. It was then found that if the square root were used instead of the actual measurement, a more or less normal distribution was obtained.(Fig. 15.)

The range for campestris was from 4.0 to about 25.0 cm., and that for multiflora and congesta was from approximately 15.0 to 75.0 cm.; for pallescens the range was between 15.0 and 30.0 cm. The overlap of the range of campestris and the other two common taxa is thus about 10 cm.

2. Leaf Length.

The total range in variation in this character was from 2.2 cm. to 22.9 cm., and the frequency distribution on a histogram followed the same general pattern as that of the stem height. Again, conversion to logarithms skewed the curve in the opposite direction, and the use of the square root produced a more normal curve.

The range for campestris was 2.2 to approximately 8.0 cm., and for _pallescens_, _congesta_ and _multiflora_ it was about 5.0 to 23 cm. There is, again, some overlap, this time of about 3.0 cm.

3. Leaf Width.

The range in variation here was from 0.09 to 0.62 cm., and the frequency histogram showed a normal distribution.

The range for _campestris_ was 0.09 - 0.25 cm., and for _multiflora_ and _congesta_ it was from 0.20 to 0.62 cm., while _pallescens_ has narrower leaves than _congesta_ and _multiflora_, but slightly broader than those of _campestris_.

It was observed that there appeared to be no significant difference in these three vegetative characters when _multiflora_ was compared with _congesta_.

4. Number of Heads per Inflorescence.

Each inflorescence consists of one sessile, terminal head and from one to 15 or more lateral heads. The latter may be on stalks 2 or 3 cm. long, or the stalks may be so short that the heads appear to be almost sessile.

In _campestris_ the number of heads varies from 2 to 6, but is usually 4 or 5. _Multiflora_ has most often 5 to 7 heads, but there may be as few as 3, or as many as 10; _pallescens_ always has a very large number of heads, usually between 10 and 15; _congesta_ generally has 5 or 6, the exact number often being difficult to determine without pulling away part of the inflorescence. (Fig. 16.)

5. Number of Flowers per Inflorescence.

The number of flowers varies from 10 or even fewer to over 100. Campestris has from 10 to 25 flowers in each inflorescence, while multiflora and congesta have between 20 and 50. Pallescens has a large number of very small flowers in each head, and the total number is usually more than 50.

This character may seem to be merely another expression of the previous one, but campestris has the smallest number of flowers in each head, as well as having the fewest heads in each inflorescence; multiflora and congesta are intermediate, while pallescens has the largest number of flowers per head, and of heads per inflorescence.

6. Stamen Length.

The length of the stamens varies from 0.84 to 2.51 mm. The stamens of campestris are the longest, ranging from about 1.50 mm. to 2.50 mm., while for multiflora and congesta they are between 1.0 and 2.0 mm., giving a considerable degree of overlap. The stamens of pallescens are usually under 1.0 mm. in length.

7. Anther : Filament Ratio.

In campestris the anther is longer than the filament, while in multiflora, congesta and pallescens it is equal to or shorter than the filament. This relationship is expressed as the ratio of the anther to the total length of the stamen, which avoids the use of a logarithmic scale. This would have been necessary had a simple anther:filament ratio been used, since values of more than and less than 1.00 would have been obtained. The range of variation is from 0.289 to 0.820, campestris ranging from about 0.550 upwards while the other three taxa are usually less than 0.550; the overlap here is much less than in any of the preceding characters. (Fig. 17.)

8. Seed Length : Width Ratio.

The seeds of campestris are more or less spherical, while those of multiflora, congesta and pallescens are all ellipsoidal. This can be expressed as a ratio by dividing the length of a seed by its width. The range of variation is from 1.04 to 1.83, campestris falling in the lower part of the range (up to about 1.40), and the other three in the upper part. The ranges again show a relatively small overlap. The length of the seed does not include the basal caruncle. (Fig. 18.)

9. Seed Size.

The size of the seeds varies, congesta having the largest and pallescens the smallest. An index of the size of the seeds was obtained by multiplying the length in mm. by the width in mm. Since this was merely an index of size, the decimal points were omitted, and the value expressed in round numbers. The range in size is from 31 to 174, representing a range in length of the seeds of from about 0.8 mm. to 1.60 mm. Pallescens has the smallest seeds, with a range of from about 30 to 60. Multiflora varies from 60 to about 120, and congesta is usually over 100. These two show a good deal of overlap, but the difference in size is very significant. Campestris seeds vary considerably in size, with a range of from about 70 to 130.

10. Perianth Length.

An inner perianth segment was always used, since the outer ones are somewhat keeled and curved, and they were more difficult to measure accurately. Campestris has flowers ranging from 3.0 to 4.0 mm. long, and they are of a dark brown colour. The flowers of congesta are between 3.0 and 4.4 mm. long, and are of a lighter shade of brown than those of campestris, while those of multiflora are similar in colour, but range in size from about 2.0 mm. to 3.5 mm. The flowers of pallescens are a pale straw colour, and they are usually less than 2.0 mm. long. The colour of the perianth was not used in the analyses, since it is too difficult to measure accurately, and it is also too readily modified by the environment.

11. Congestion of the Inflorescence.

The degree of congestion of the inflorescence ("congestion index") was determined by measuring the length of the stalks of all the heads of each inflorescence, and then calculating the mean length, which is the index, and is expressed in cm. This may not be an altogether satisfactory method, especially when the inflorescence has one or two heads on long stalks, with the rest sessile. It is a relatively simple calculation, and the size of the samples made it essential to omit any unnecessary arithmetical complications; also, in the vast majority of cases, this index gave a true picture of the relative degree of congestion of the inflorescence. (Fig. 16).

The total range of variation is from 0.11 cm. to 2.72 cm., and when plotted on a frequency histogram the distribution is very much skewed towards the lower end of the scale. However, the use of a logarithmic scale, or of logarithmic graph paper produced a more or less normal distribution, (Fig. 19). The range for congesta is from 0.10 cm. to 0.40 cm., while multiflora and pallescens may be as low as 0.50 cm., but are usually over 0.8 cm.; values of the congestion index of over 2.00 cm. are rare. Campestris ranges from 0.30 cm. to about 1.50 cm., and is seldom more.

The range of multiflora and congesta in this character shows little or no overlap, though a few plants with intermediate values do occur.

It is seen that each of these characters shows a considerable degree of variation. The majority of them show a normal distribution, but stem height and leaf length require to be converted to the square root before a normal curve is obtained, while the congestion index shows a logarithmic distribution. Some particular examples of the type of variation seen in these characters will be considered in the next section, in order to illustrate them, and to demonstrate the variation of different characters within a single population and between groups of populations. The effect of environment on certain features of the plants will also be discussed.

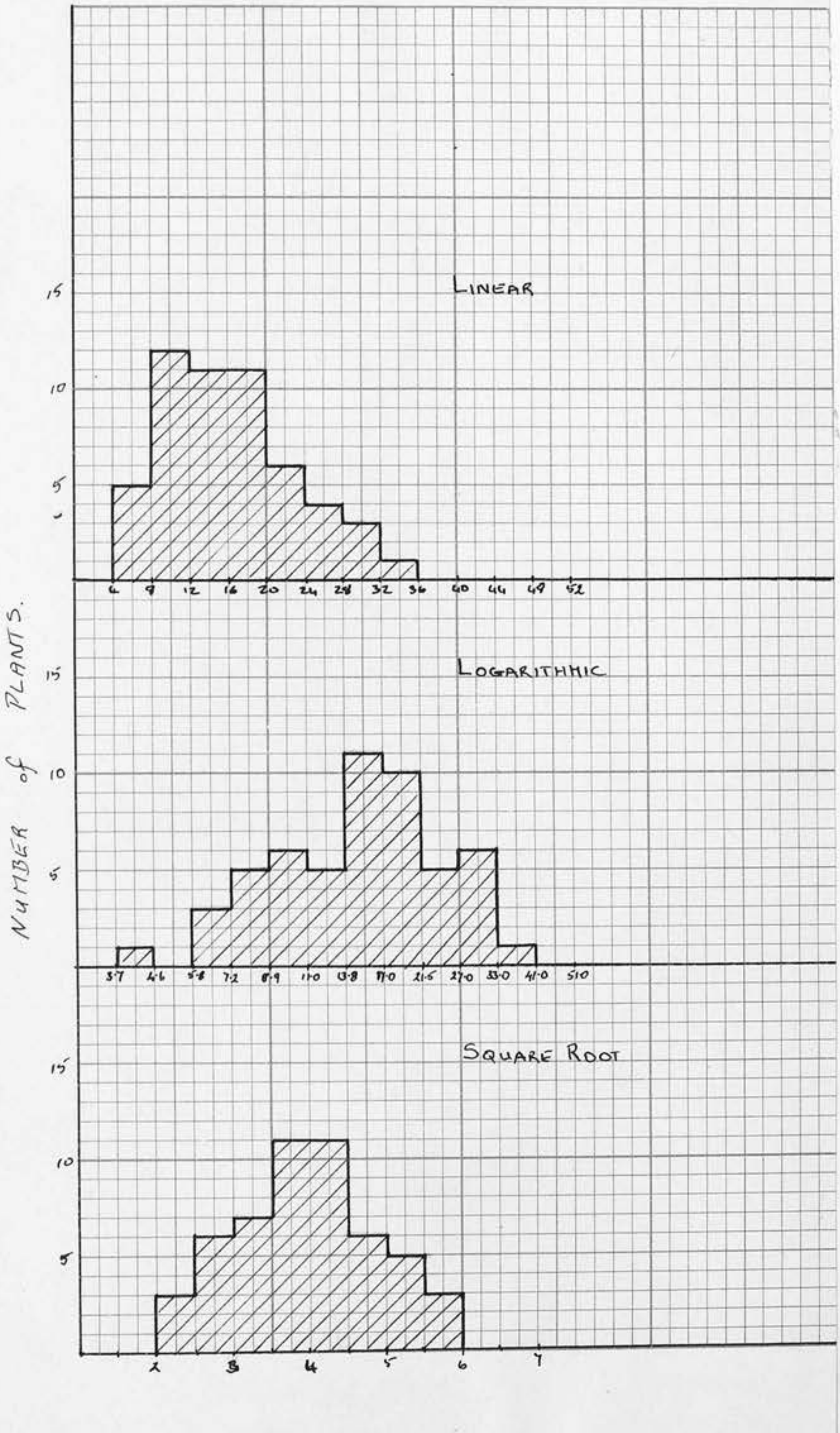
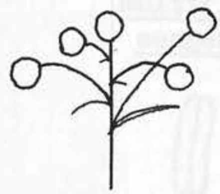
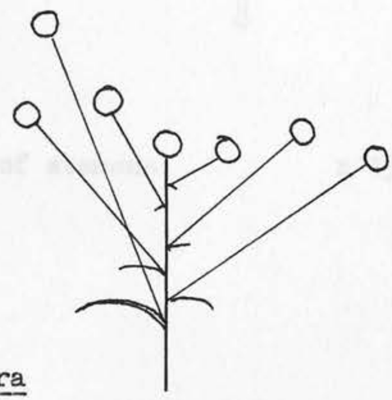


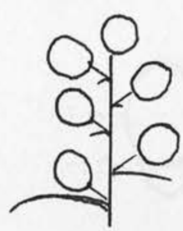
Fig. 15. Frequency histograms of H, log H and $\sqrt{H}$.



1. <u>campestris</u>



2. <u>multiflora</u>



3. <u>congesta</u>

Fig. 16. Diagrams of inflorescences. The main axis is extended to clarify the relationships of the branches.

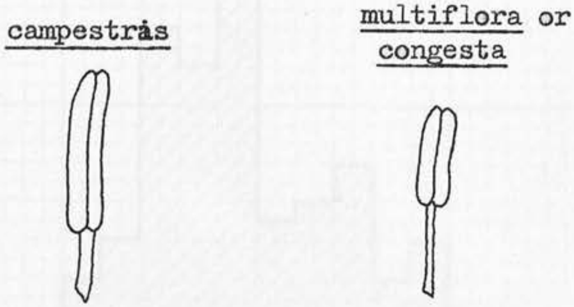


Fig. 17. Diagram of stamens. x 15

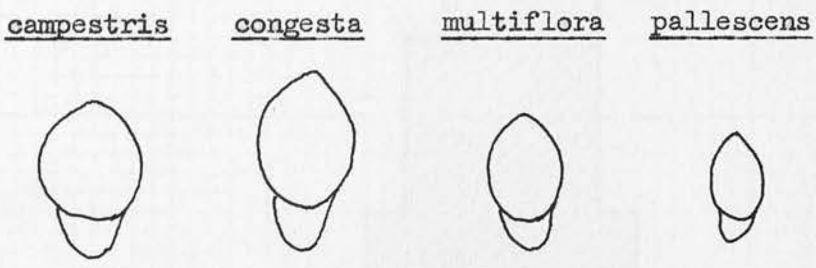


Fig. 18. Diagram of seeds. x 15

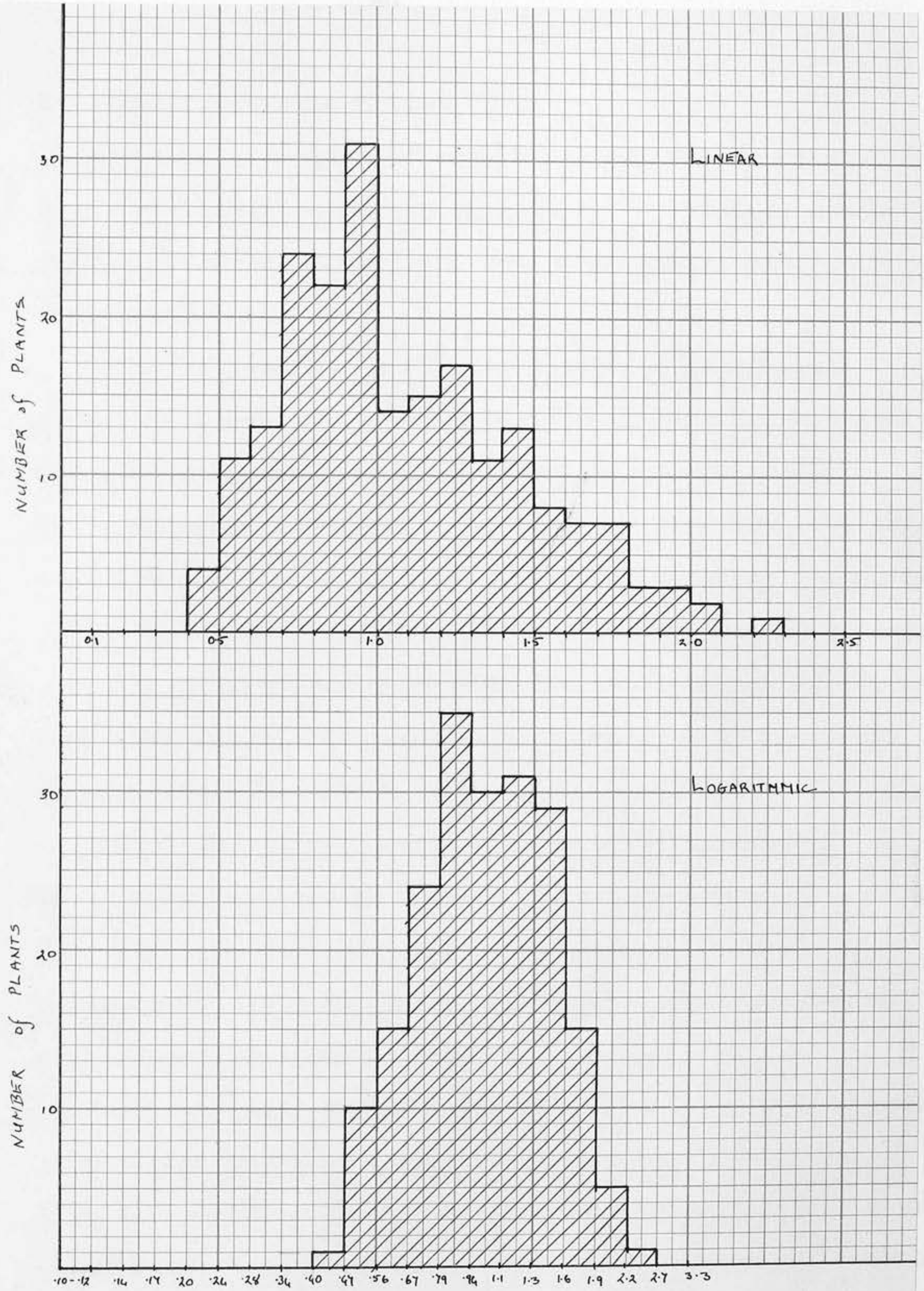


Fig. 19. Frequency histogram of S and log S.

D. INTER-RELATIONSHIPS OF CHARACTERS.

A summary of the range of variation of each character in every population measured is given in Appendix I. The maximum, minimum and mean are given for each, and the standard deviation and variance where appropriate.

There are variations in the relationships of the different characters to each other; some show a positive correlation, others a negative correlation, while others are not correlated at all. It is reasonable to expect that the vegetative characters will show a positive correlation, which can in fact be satisfactorily demonstrated.

The leaf length and leaf width show a positive correlation, both when only one population of one taxon is considered, and when two or more populations of different taxa are compared, as in the scatter diagrams, figs. 20 ~~a and b~~.

Stem height and leaf length also show a positive correlation. If the actual measurements are used, the scatter diagram has a slightly "fan-like" appearance, the scatter being greater for the larger measurements. If $\sqrt{H}$ and $\sqrt{L}$ are used, however, the scatter becomes more or less spindle-shaped (Figs. 21 ~~a and b~~).

These vegetative characters may be modified by the environmental conditions. When plants of multiflora and congesta are growing along tall rushes and grasses they tend to be approximately the same height as the surrounding plants. When they are growing with smaller grasses they tend to be smaller also. This may be the effect of soil conditions rather than of the associated plants, since the former type pf habitat is generally more moist than the latter. Plants of campestris may be 8" to over 1 foot tall if they are growing in a favourable habitat, and are not subject to grazing. Where grazing is heavy the flowering stems may be only 4 - 5 inches high, and plants of this taxon growing in lawns have flowering stems of only 1 or 2 inches (but here it is not certain whether they ever ripen seed). Care must also be taken to ensure that the plants are all of a comparable age when using vegetative characters, since the flowering stems more than double their height between flowering and the ripening of the seeds; it is therefore necessary to collect all the plants when the seed is ripe, and they have reached their maximum height. The only time when vegetative features can validly be used as taxonomic characters in this group of plants is when the plants concerned are all grown under identical conditions of cultivation.

A few scatter diagrams will help to illustrate the variation in the vegetative characters. Figure 22 shows the scatter diagram obtained when L and B are plotted against each other. This sample is composed of congesta and multiflora; the stem height and leaf length for the same sample are plotted in Fig. 23, and both diagrams show a strong positive correlation. When a sample of campestris is compared with the same congesta/multiflora sample the positive correlation is maintained, with some overlap between the taxa; there is only a slight suggestion of a break between the two groups.

Another pair of characters which show a positive correlation are the number of heads in the inflorescence, and the number of flowers in the inflorescence. The ratio of these to each other varies with the taxa, and a better correlation might be obtained by comparing the number of heads with the average number of flowers per head. (Fig.25).

When the length of the anther and the length of the filament are plotted against each other, the correlation tends to be negative, campestris having a different ratio of a:f from the other taxa. (Fig.26).

Seed length and seed width show a positive correlation in all the taxa, but the difference in ratio between campestris and the other taxa is even more marked that it is for the stamen characters, and congesta has larger seeds than multiflora. (Fig. 27).

The last two features are best expressed as ratios if they are to be used to separate campestris from congesta and multiflora. When the ratios seed-length: seed-width and anther: total stamen length (s/w and $\frac{a}{a + f}$) are plotted against each other a negative correlation might be expected. This is in fact very slight within the taxa, and when two different taxa are present (i.e. campestris and multiflora or congesta) they fall into two more or less distinct groups on the diagram. Only if there is a relatively large number of intermediate (?hybrid) forms in the sample is there any real sign of a negative correlation. (Figs. 28 a and b).

The characters separating congesta and multiflora also show different types of relationship. The seed size (s x w) and petal length show a positive correlation, congesta being larger in both characters; the variation is continuous, with a considerable amount of overlap between the taxa. (Fig. 29).

The congestion index, on the other hand, shows a negative correlation with both the previous characters, and there is a separation into two groups of plants, as the intermediate values of S are infrequent, although the other characters show considerable intergradation. The scatter diagrams of S: s x w, and S : P are plotted on logarithmic graph paper, in order to avoid the conversion of all the values of S to logarithms.

Figure 30 shows the scatter diagram of S and s x w for two mixed populations of multiflora and congesta. The negative correlation is not very well marked, but it can be seen that the plants with low values of S have larger seeds (congesta) than those with high values of S (multiflora). If more or less pure populations of congesta and multiflora are treated in the same way the groups are even more distinct, and the congesta group has a mean value of S considerably higher than that of the multiflora group; in this case the intermediate values of S are even less frequent than in the former, and no negative correlation is seen. (Fig. 30b). Scatter diagrams of S and P show a similar pattern of variation.

If these three characters are combined in one diagram, by the use of different symbols for values of S above and below 0.50 cm. superimposed on the scatter diagram of s x w and P for the same group of plants, it is seen that the plants with a low value of S (congesta) are at the upper end of the scale, while the high values of S (multiflora) are at the lower end (Fig. 31). This demonstrates the interrelationship of the three characters.

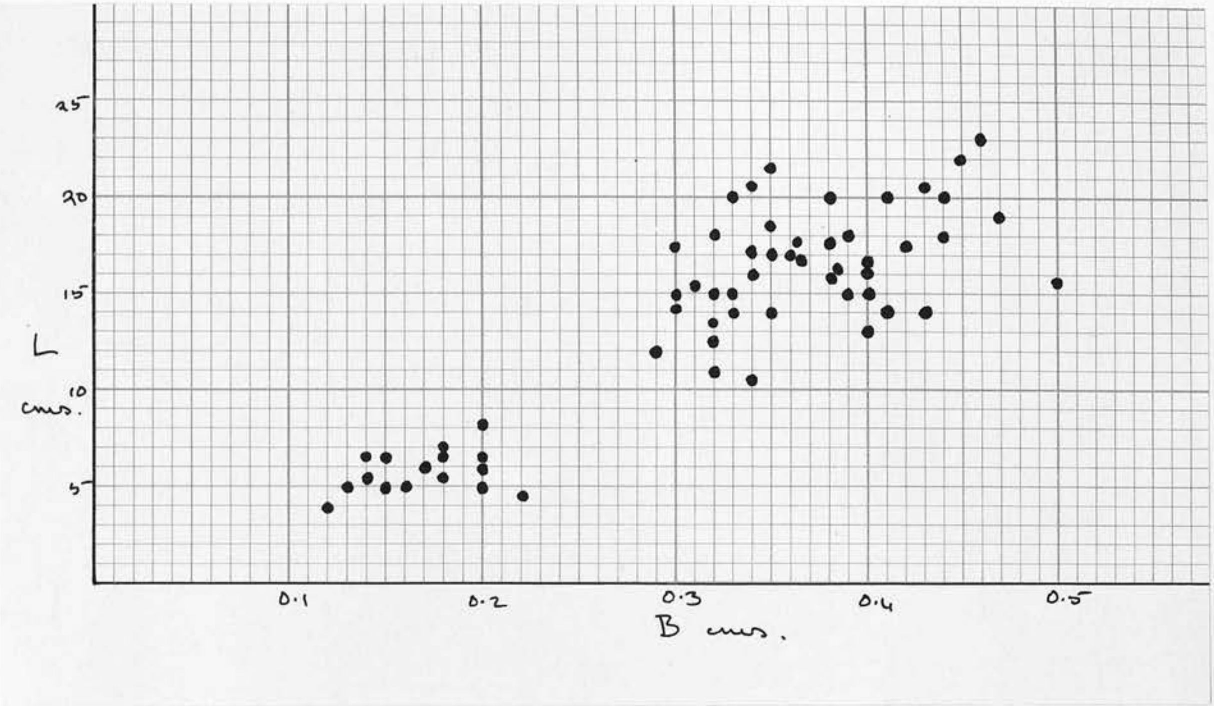


Fig. 20. Scatter diagram of leaf length and leaf width.

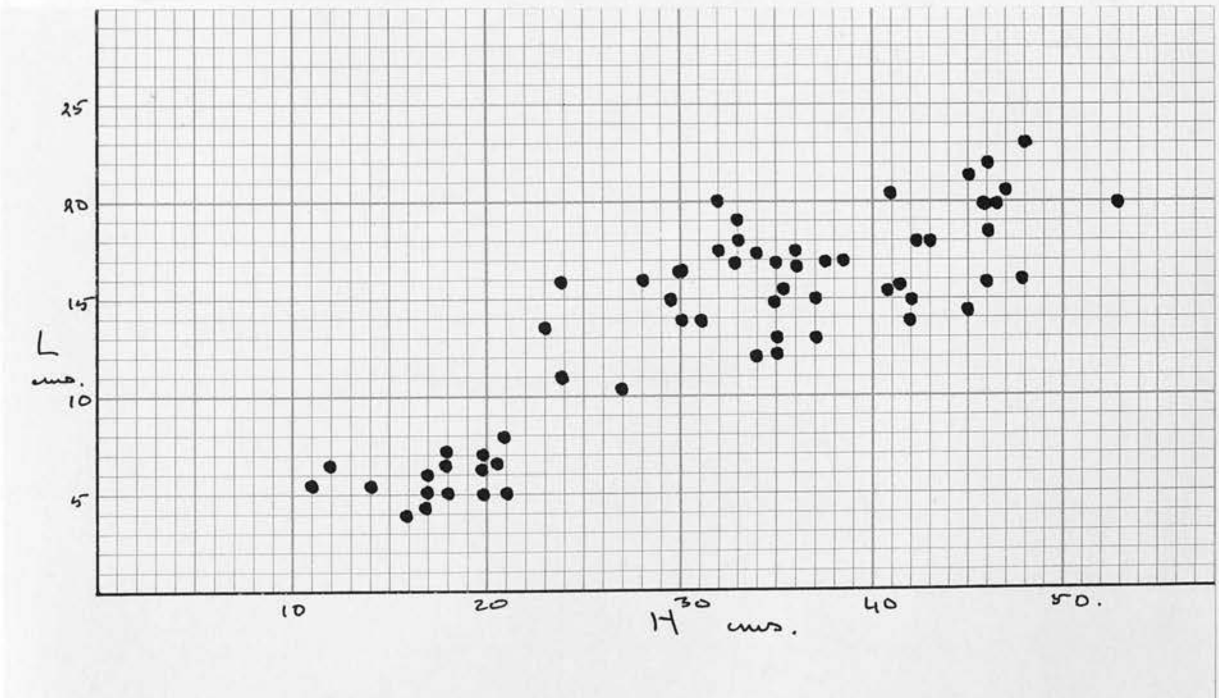


Fig. 21. Scatter diagram of leaf length and stem height.

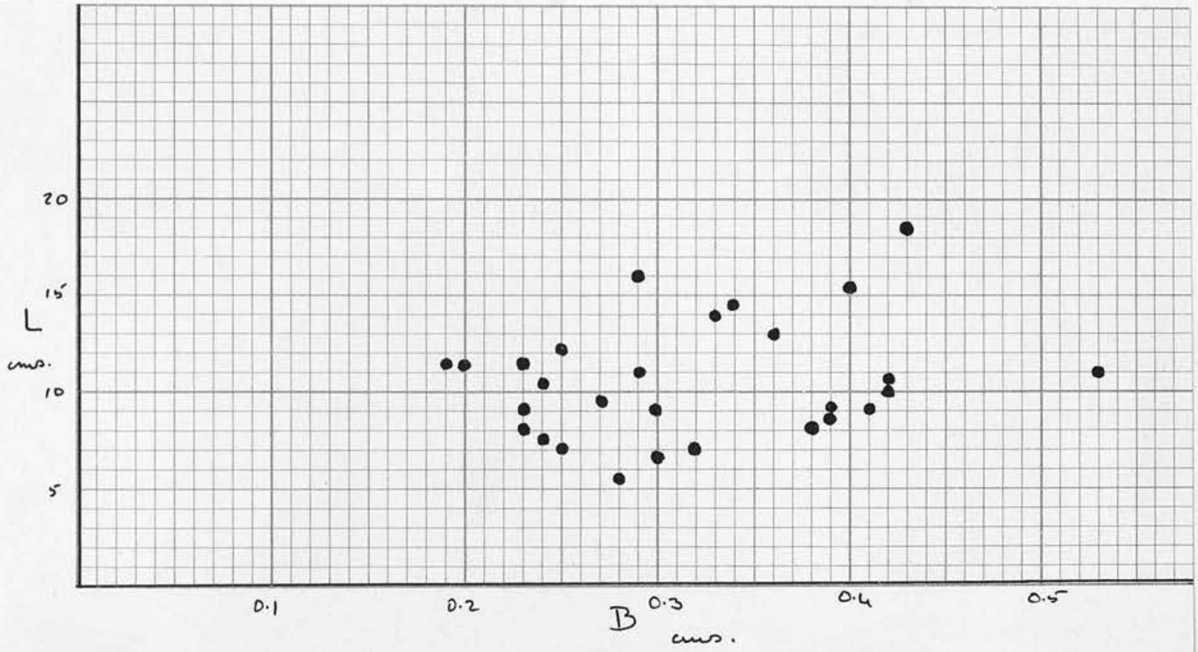


Fig. 22. Scatter diagram of L and B for a mixed population of
multiflora and congesta.

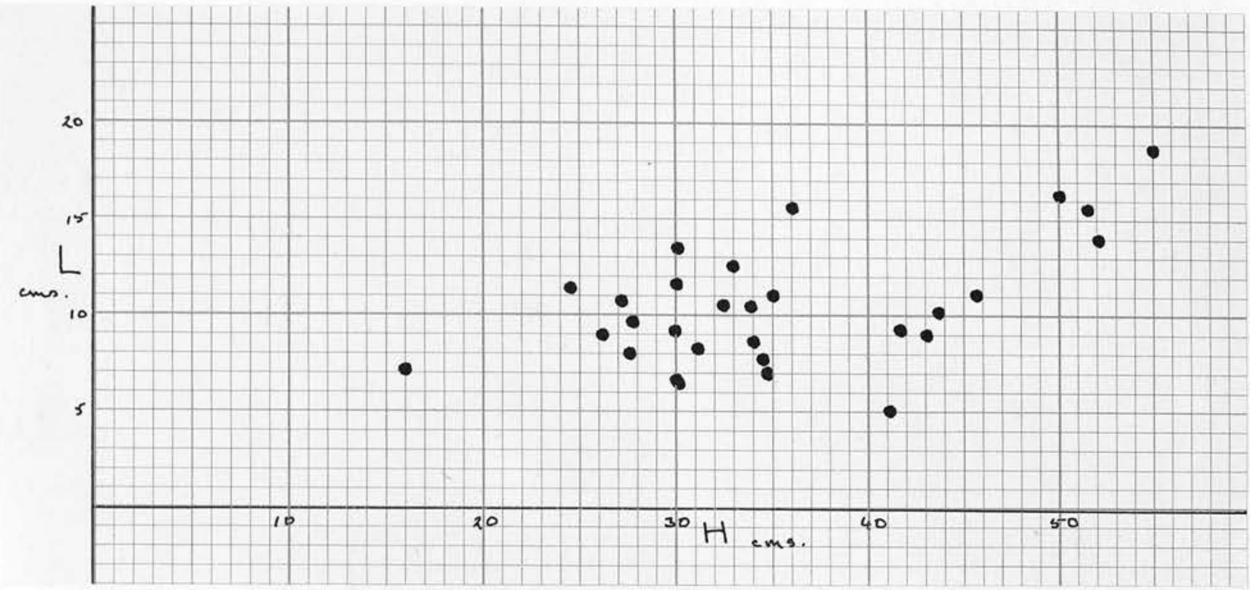


Fig. 23. Scatter diagram of L and H for the same plants as fig. 22.

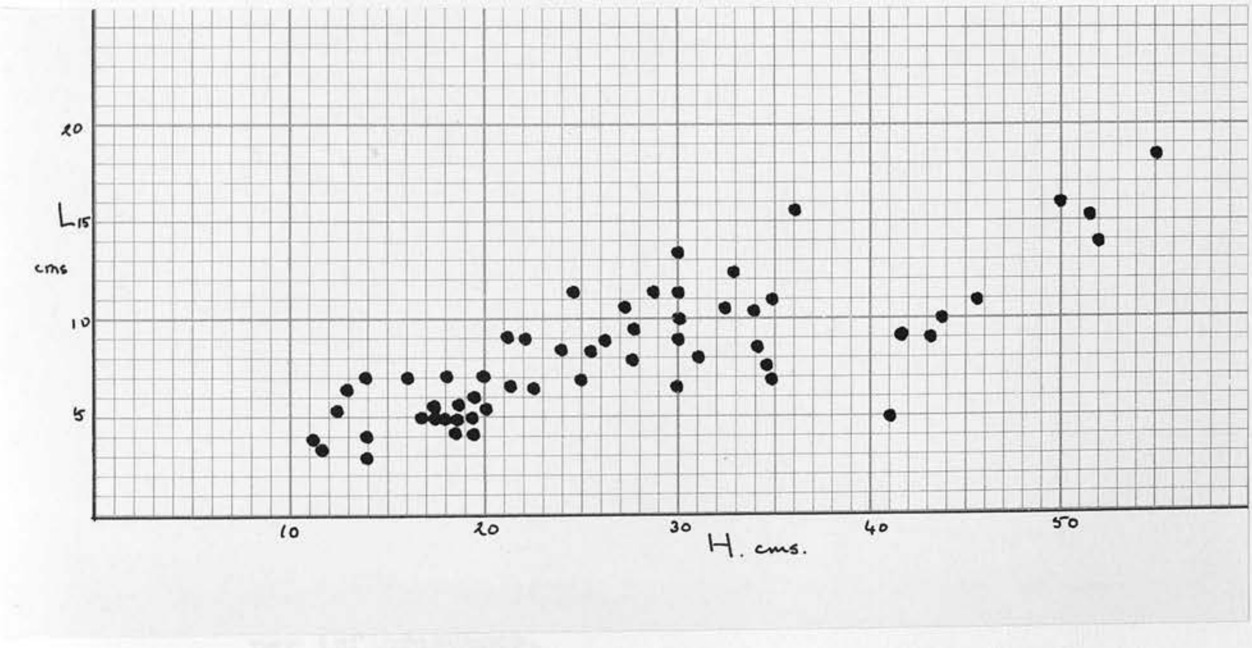


Fig. 24. Scatter diagram of L and H as in fig. 23, but with a population of campestris included.

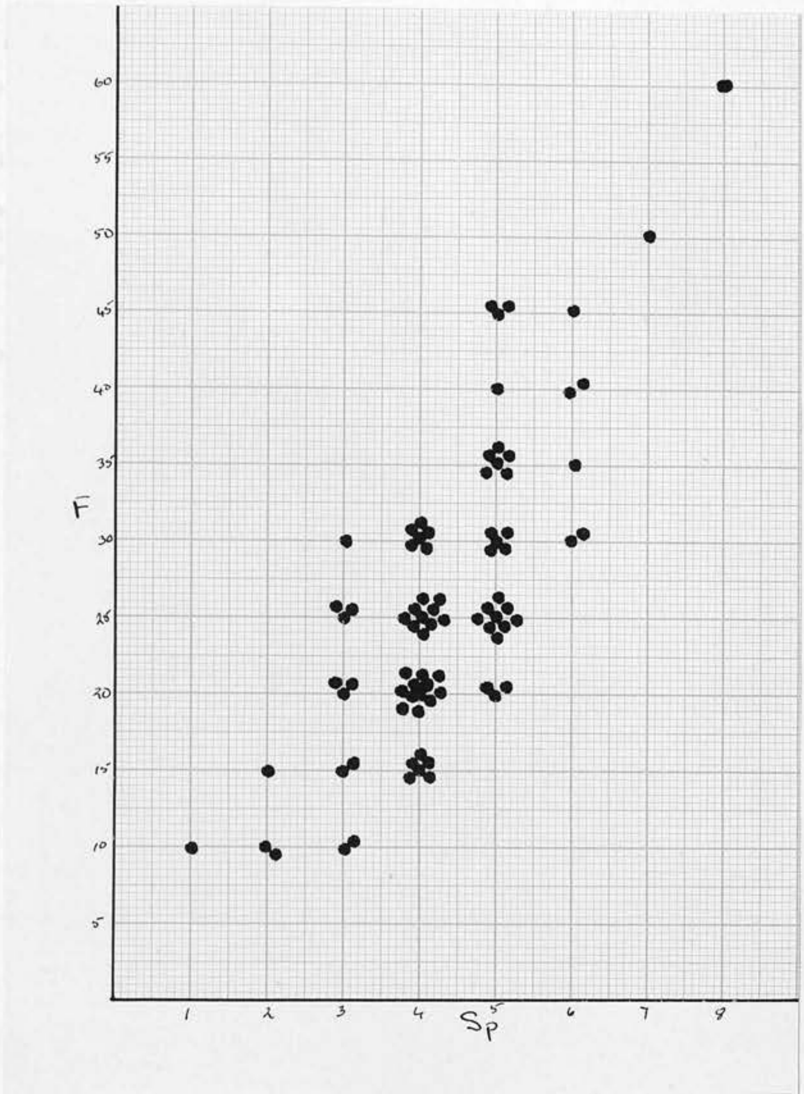


Fig. 25. Scatter diagram of the number of heads (Sp) and of flowers (F) per inflorescence.

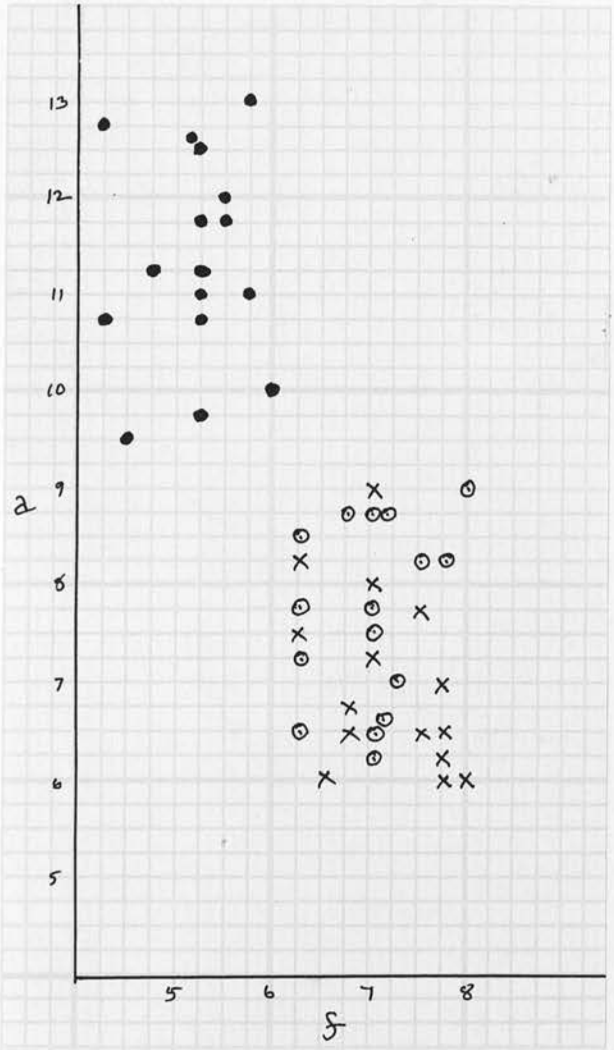


Fig. 26

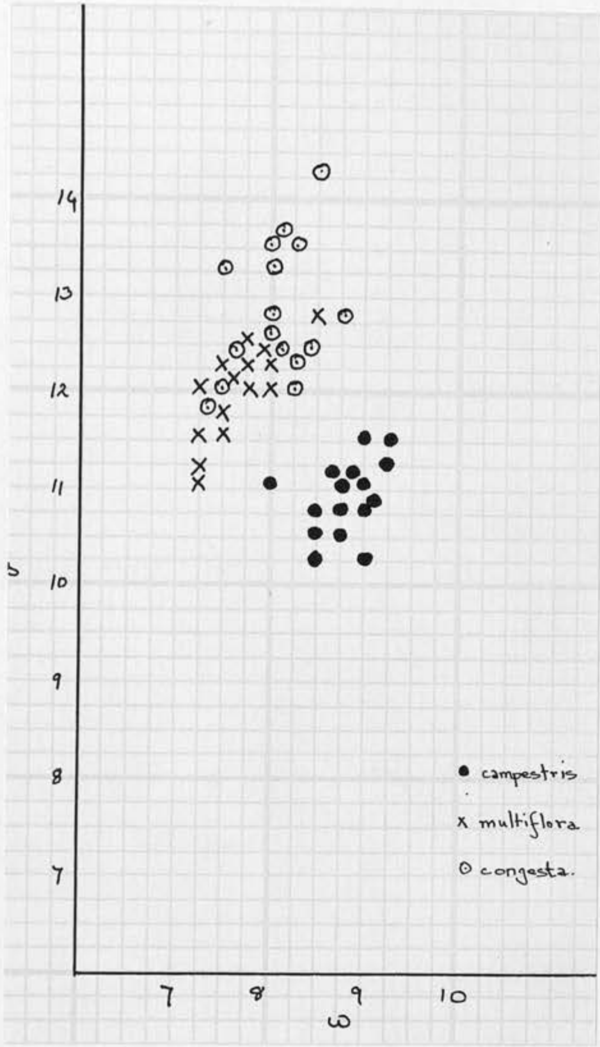
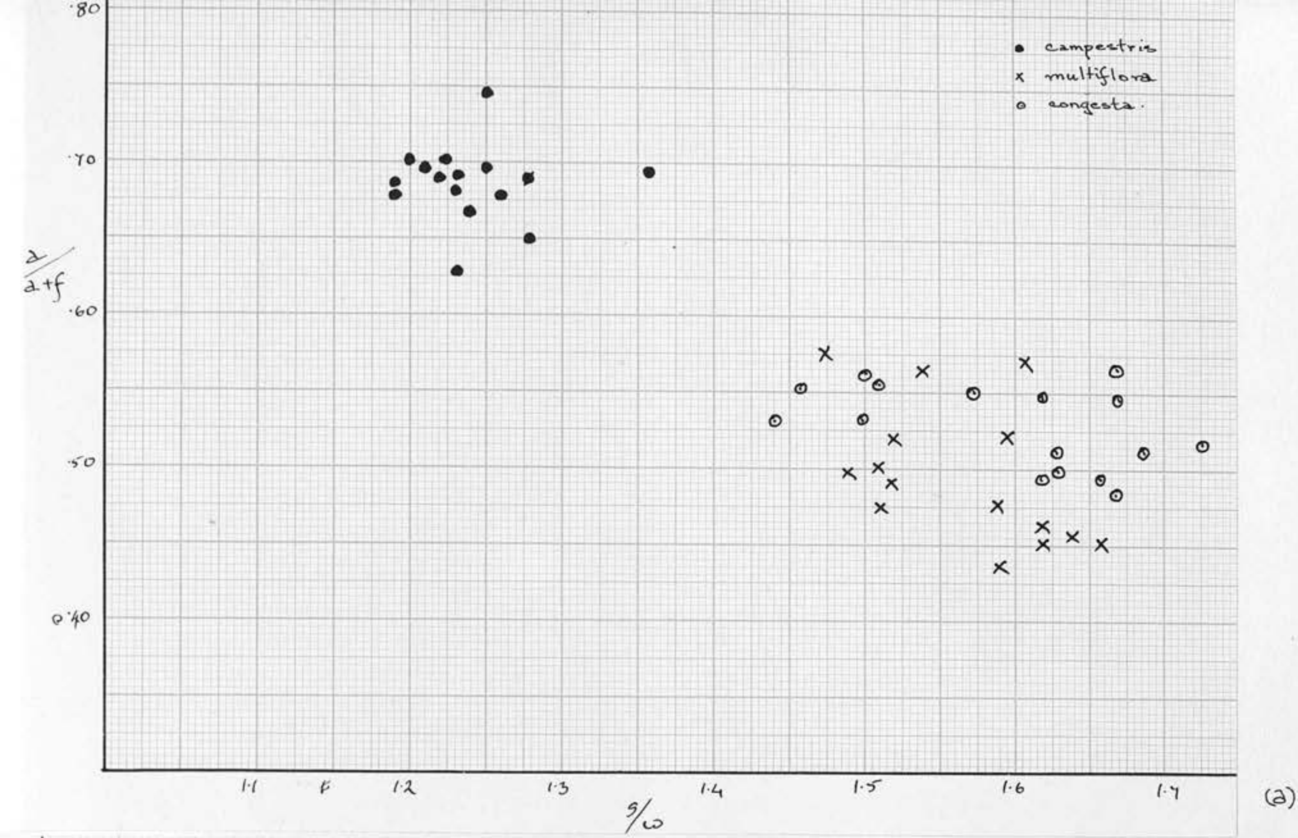


Fig. 27

Fig. 26. Scatter diagram of anther length (a) and filament length (f).

Fig. 27. Scatter diagram of seed length (s) and seed width (w).



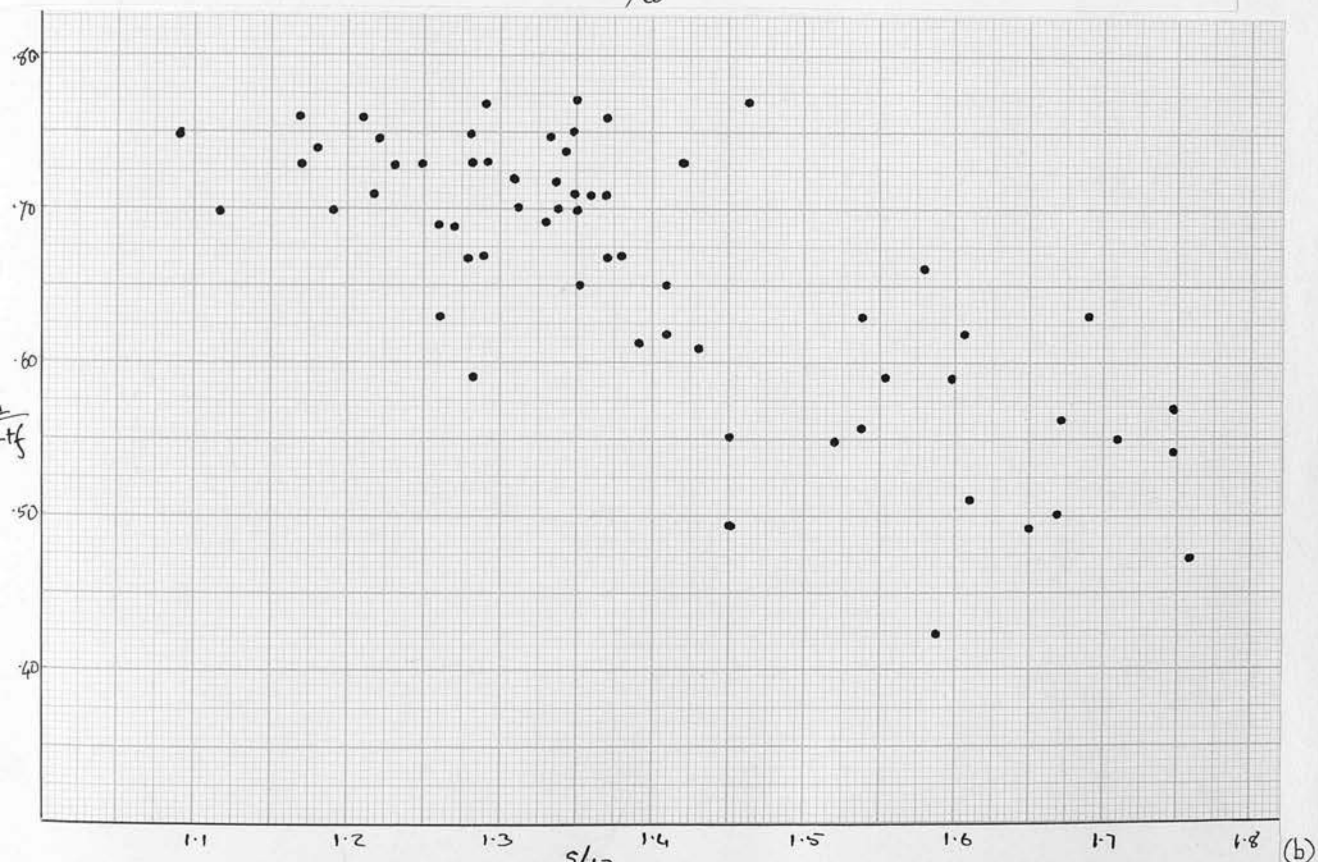


Fig. 28. Scatter diagram of $\frac{a}{a + f}$ and s/w for

a) pure populations of campestris, multiflora and congesta.

b) populations with possible hybrids.

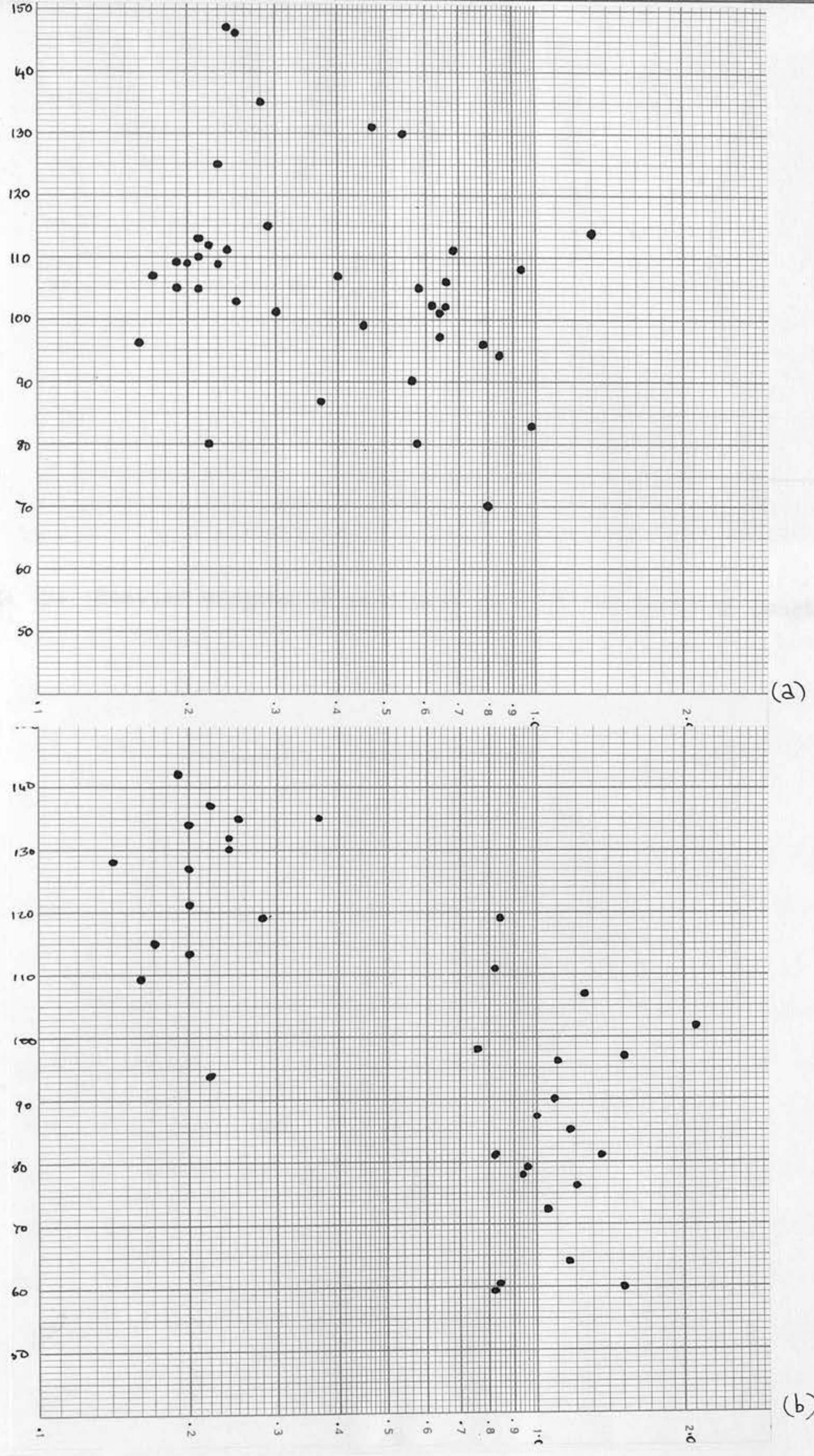


Fig. 30. Scatter diagram of congestion index and seed size.
a) mixed population of <u>multiflora</u> and <u>congesta</u>.
b) two pure populations of <u>multiflora</u> and <u>congesta</u>.

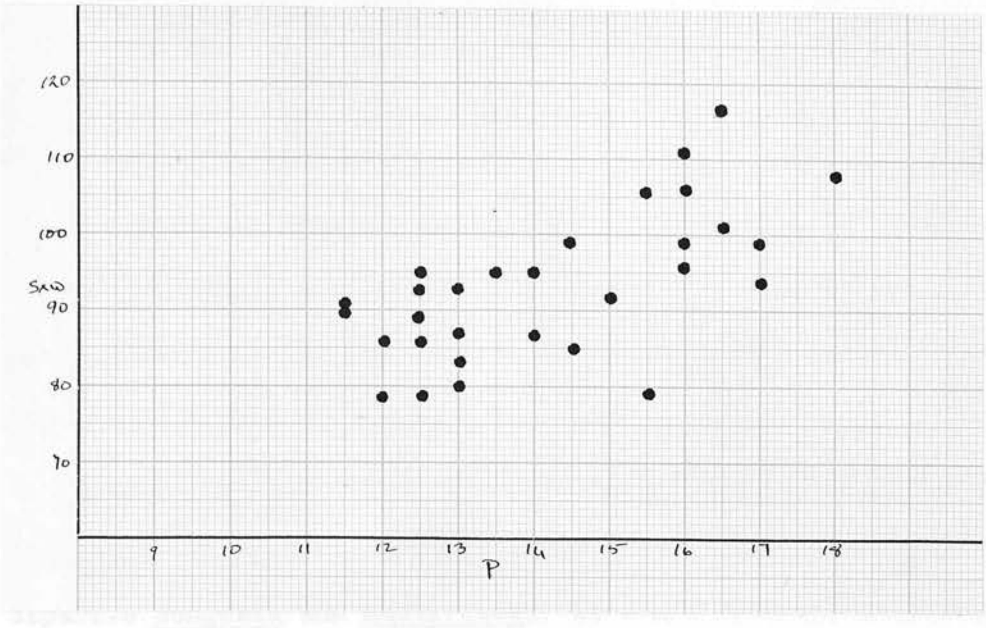


Fig. 29. Scatter diagram of seed size (s x w) and perianth length (P).

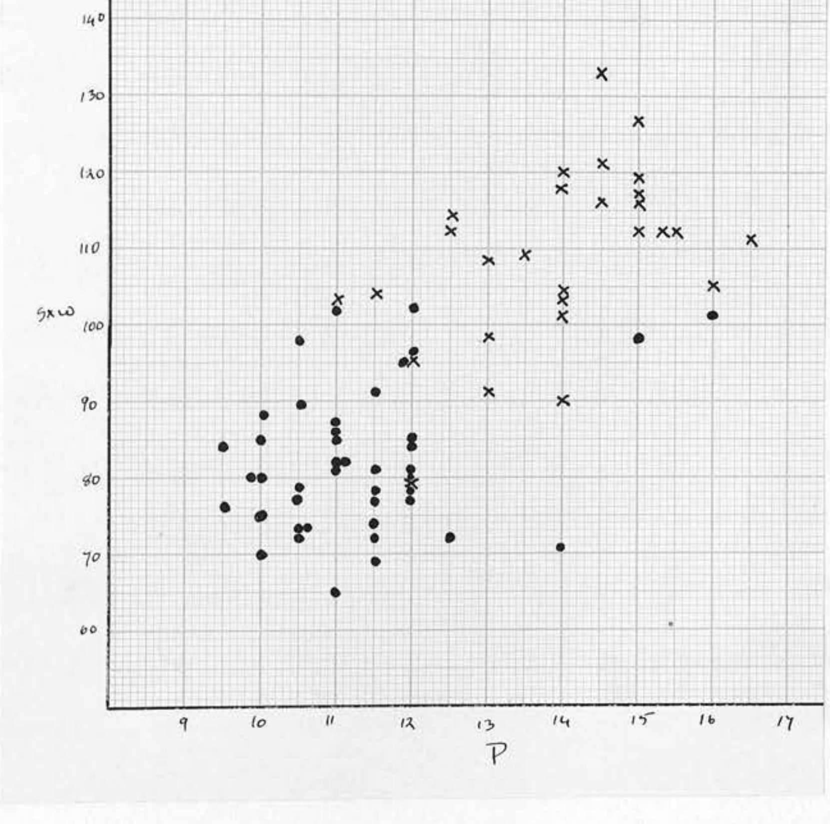


Fig. 31. Scatter diagram of s x w and P, with S superimposed.
x = S greater than 30, o = S less than 30

E. INDICES.

The previous sections dealt with the variation in individual characters within and between the taxa. It is seen that the total range of each character is considerable, and that the different taxa may occupy different parts of the range.

Five floral characters separate campestris from multiflora and congesta; F, Sp, a + f, $\frac{a}{a + f}$, and s/w. Three floral characters separate congesta and multiflora; S, s x w and P. In each case, no one character was sufficient to separate any of the taxa from the others, although $\frac{a}{a + f}$ and s/w could be used together to give a reasonable separation into two groups (campestris and multiflora + congesta), while the two latter taxa can usually be separated by the degree of congestion of the inflorescence.

It was considered desirable to devise a method whereby all three groups of plants could be compared at the same time, and which would utilise all the available diagnostic characters.

Methods of combining characters numerically to give indices have frequently been used by botanists. The simplest of these is probably the "Hybrid Index" (Riley 1938, Anderson 1953). In this method, each of the diagnostic characters is scaled 0, 1 or 2, according to whether it is characteristic of one or other of the species concerned, or whether it is intermediate between them. For this method to be applicable, the two species concerned must be reasonably distinct to start off with, as the range of variation on the scale is necessarily rather limited. For the same reason, it is also desirable that there should be a considerable number of diagnostic characters, i.e. at least six, and preferably ten or more. An advantage of the "Hybrid Index" is that it can make use of characters which it is difficult to measure at all accurately - e.g. flower colour.

On the whole, however, a rather more complex type of index seemed to be required in the present case, since there were few really good diagnostic characters, each of which showed a considerable range of variation, but all of which it was possible to measure with a fair degree of accuracy.

The total range of variation of each character was estimated from all the plants measured, including both the mass gatherings and the herbarium specimens, and also including pallescens, where this taxon extended the range in either direction.

These ranges of variation were then divided into 50 units. In most cases, the divisions were on a straight-forward arithmetic scale, i.e. in F, Sp, a + f, $\frac{a}{a + f}$, s/w, s x w, and P. The ranges of variation of the vegetative characters were also divided into 50 units, but in this case only B was divided on an arithmetic scale, a square root scale being used for H and L. This was because of the type of variation shown by these characters (see fig. 15), and to have divided them arithmetically would have resulted in effectively unequal divisions. In the case of S, the divisions were logarithmic, as this was the type of variation shown by the character in the frequency histograms (see fig. 19).

These divisions are given in tables 6, 7 and 8. Table 6 contains the three vegetative characters, H, L and B. Table 7 contains the five characters which separate campestris from multiflora and congesta, while table 8 contains the three characters separating congesta and multiflora.

In table 6, each scale starts at the lowest and ends at the highest value for each of the characters, since they all show a positive correlation.

In table 7, F and Sp do not show enough range of variation to make possible the division of the ranges into 50 parts, so they are divided into 25 units, and these correspond to every alternative division of the other characters. The characters F, Sp and s/w all show a positive correlation, but a + f and $\frac{a}{a + f}$ show a negative correlation with them, so that, while the three former start at the lowest part of the range, the other two characters are reversed, so that all the values typical of campestris come at the lower end of the scale, while all those typical of multiflora and congesta come at the upper end.

In table 8, s x w and P show a positive correlation with each other, and a negative correlation with S, the range of which has therefore been reversed, so that all the values typical of congesta are at the upper end of the scale, with those typical of multiflora at the lower end.

Using these three tables, each character can be converted to its corresponding value on the scale 0 - 50. The converted values can

TABLE 6

CONVERSION TABLE FOR CHARACTERS IN Z INDEX

index value	H cm.	L cm.	B cm.	index value	H cm.	L cm.	B cm.
1	2.25	1.00	0.05	26	27.56	9.00	.400
2	2.72	1.17	.064	27	29.16	9.49	.414
3	3.24	1.35	.078	28	30.80	9.98	.428
4	3.80	1.54	.092	29	32.49	10.49	.442
5	4.41	1.74	.106	30	34.22	11.02	.456
6	5.06	1.96	.120	31	36.00	11.56	.470
7	5.76	2.19	.134	32	37.82	12.11	.484
8	6.50	2.43	.148	33	39.69	12.67	.498
9	7.29	2.69	.162	34	41.60	13.25	.512
10	8.12	2.96	.176	35	43.56	13.84	.526
11	9.00	3.24	.190	36	45.56	14.44	.540
12	9.92	3.53	.204	37	47.61	15.05	.554
13	10.89	3.84	.218	38	49.70	15.68	.568
14	11.90	4.16	.232	39	51.84	16.32	.582
15	12.96	4.49	.246	40	54.02	16.97	.596
16	14.06	4.84	.260	41	56.25	17.64	.610
17	15.21	5.19	.274	42	58.52	18.32	.624
18	16.40	5.57	.288	43	60.84	19.01	.638
19	17.64	5.95	.302	44	63.20	19.71	.652
20	18.92	6.35	.316	45	65.61	20.43	.666
21	20.25	6.76	.330	46	68.06	21.16	.680
22	21.62	7.18	.344	47	70.56	21.90	.694
23	23.04	7.62	.358	48	73.10	22.66	.708
24	24.50	8.07	.372	49	75.69	23.42	.722
25	26.01	8.53	.386	50	78.32-81.00	24.20-25.00	.736-.750

TABLE 7

CONVERSION TABLE FOR CHARACTERS IN THE X INDEX

index value	F	Sp	a + f	$\frac{a}{a + f}$	s/w
1			2.70	0.900	1.00
2	I	1	2.66	.886	1.02
3			2.62	.872	1.04
4	II	2	2.58	.858	1.06
5			2.54	.844	1.08
6	III	3	2.50	.830	1.10
7			2.46	.816	1.12
8	IV	4	2.42	.802	1.14
9			2.38	.788	1.16
10	V	5	2.34	.774	1.18
11			2.30	.760	1.20
12	VI	6	2.26	.746	1.22
13			2.22	.732	1.24
14	VII	7	2.18	.718	1.26
15			2.14	.704	1.28
16	VIII	8	2.10	.690	1.30
17			2.06	.676	1.32
18	IX	9	2.02	.662	1.34
19			1.98	.648	1.36
20	X	10	1.94	.634	1.38
21			1.90	.620	1.40
22	XI	11	1.86	.606	1.42
23			1.82	.592	1.44
24	XII	12	1.78	.578	1.46
25			1.74-1.70	.564-.550	1.48-1.50

TABLE 7 (continued)

index value	F	Sp	a + f	$\frac{a}{a + f}$	s/w
26	XIII	13	1.70	0.550	1.50
27			1.66	.536	1.52
28	XIV	14	1.62	.522	1.54
29			1.58	.508	1.56
30	XV	15	1.54	.494	1.58
31			1.50	.480	1.60
32	XVI	16	1.46	.466	1.62
33			1.42	.452	1.64
34	XVII	17	1.38	.438	1.66
35			1.34	.424	1.68
36	XVIII	18	1.30	.410	1.70
37			1.26	.396	1.72
38	XIX	19	1.22	.382	1.74
39			1.18	.368	1.76
40	XX	20	1.14	.354	1.78
41			1.10	.340	1.80
42	XXI	21	1.06	.326	1.82
43			1.02	.312	1.84
44	XXII	22	0.98	.298	1.86
45			.94	.284	1.88
46	XXIII	23	.90	.270	1.90
47			.86	.256	1.92
48	XXIV	24	.82	.242	1.94
49	XXV		.78	.228	1.96
50	XXV	25	.74- .70	.214- .200	1.98- 2.00

TABLE 8

CONVERSION TABLE FOR CHARACTERS IN THE Y INDEX

index value	S cm.	s x w	P mm.	index value	S cm.	s x w	P mm.
1	3.162	35	1.40	26	0.562	110	2.90
2	2.951	38	1.46	27	.525	113	2.96
3	2.754	41	1.52	28	.490	116	3.02
4	2.570	44	1.58	29	.457	119	3.08
5	2.399	47	1.64	30	.427	122	3.14
6	2.239	50	1.70	31	.398	125	3.20
7	2.089	53	1.76	32	.372	128	3.26
8	1.950	56	1.82	33	.347	131	3.32
9	1.820	59	1.88	34	.324	134	3.38
10	1.698	62	1.94	35	.302	137	3.44
11	1.585	65	2.00	36	.282	140	3.50
12	1.479	68	2.06	37	.263	143	3.56
13	1.380	71	2.12	38	.246	146	3.62
14	1.288	74	2.18	39	.229	149	3.68
15	1.202	77	2.24	40	.214	152	3.74
16	1.122	80	2.30	41	.199	155	3.80
17	1.047	83	2.36	42	.186	158	3.86
18	0.977	86	2.42	43	.174	161	3.92
19	.912	89	2.48	44	.162	164	3.98
20	.851	92	2.54	45	.151	167	4.04
21	.794	95	2.60	46	.141	170	4.10
22	.741	98	2.66	47	.132	173	4.16
23	.692	101	2.72	48	.123	176	4.22
24	.646	104	2.78	49	.115	179	4.28
25	.603	107	2.84	50	.107-.100	182-185	4.34-4.40

then be added together to give three indices for each plant. These indices have been termed X (table 7), Y (table 8) and Z (table 6).

The maximum possible range for X is from 0 to 250 units, while for Y and Z it is from 0 to 150. It might seem undesirable to compare indices which differ in the number of characters used to construct them, but it is found that the actual range of variation of X, Y and Z are considerably less than their possible ranges, and that the three indices are comparable in this respect, as is shown in the table below.

	Max.	Min.	Actual range (units)	Possible range
X	177	47	130	0 - 250
Y	129	19	110	0 - 150
Z	128	17	111	0 - 150

The actual range of variation of X is very much less than its possible range; this is probably because of the characters used, particularly F and Sp. These seldom have a value of much over 30 on the scale, except in the case of pallescens, which has large numbers of very small flowers in numerous heads. The scale has therefore to be considerably extended to allow for the inclusion of pallescens in the scheme of indices. The other characters of pallescens also tend to be in the upper part of the scale, but do not cause any significant degree of extension.

The actual range of each index seems to be the important factor, and these are sufficiently similar (130, 110 and 111) to be comparable. The use of five characters for one index, and of three for the other two appears to be justified on this basis.

The index X is used to separate campestris from the other three taxa. It was worked out for every plant from all the mass gatherings. A frequency histogram of the results was constructed (fig. 32). This shows a bimodal distribution of the index values, with the modes at about 65 and 110. The curves are continuous, but there are fewest plants at a value of about 80. The smaller group of plants with the lower index value represents campestris, while the other, larger group represents multiflora and congesta, with pallescens in the extreme upper part of the range. The range of X for campestris can therefore be taken as being from 47 to about 80, and that of multiflora and congesta as from about 80 to 140; values of over 140 are typical of pallescens. The range for campestris is considerably less than that of the other taxa; this is probably due to the smaller sample.

Further analysis of the X index, considering multiflora and congesta separately, shows a slight difference between these taxa, (Fig. 42b); the value for multiflora being slightly greater than that for congesta. This effect is probably caused by the fact that the characters of number of flowers and number of heads in the inflorescence are included in the X index. They are slightly more in multiflora than they are in congesta, and affect the index accordingly.

Using the frequency histograms to provide the approximate ranges of the taxa, the variance and standard deviation of X were worked out for the four taxa. The results are summarised below.

The standard deviation, s, isthe square root of the variance , s^2, Since the samples are large, with the exception of pallescens, σ and σ^2 will be very nearly equal to s and s^2, so that the application of Bessel's correction to the formula is possibly unnecessary, in most instances.

$$s^2 \text{ (variance)} = \frac{\Sigma(x - \bar{x})^2}{n} = \frac{\Sigma x^2}{n} - \bar{x}^2$$

$$s \text{ (standard deviation)} = \sqrt{\frac{\Sigma(x - \bar{x})^2}{n}}$$

$$\hat{\sigma} \text{ (best estimate of } \sigma) = \sqrt{\frac{\Sigma(x - \bar{x})^2}{n - 1}}$$

$\hat{\sigma} = (\frac{n}{n-1})s$; where n is very large, $\frac{n}{n-1}$ is very close to unity, so that $\hat{\sigma}$ and s are approximately the same, and the application of the correction makes no significant difference to the result.

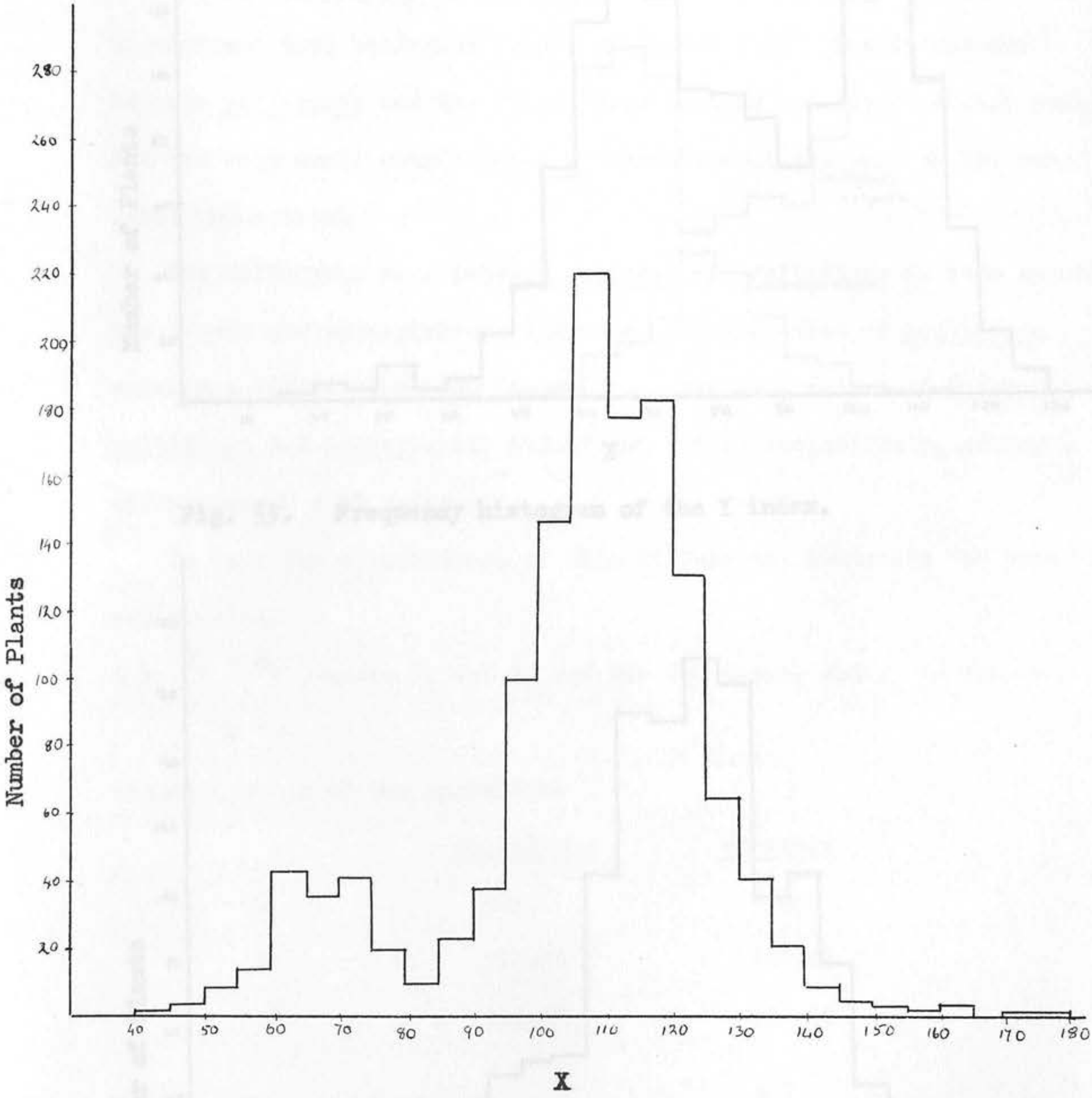


Fig. 32. Frequency histogram of the X index.

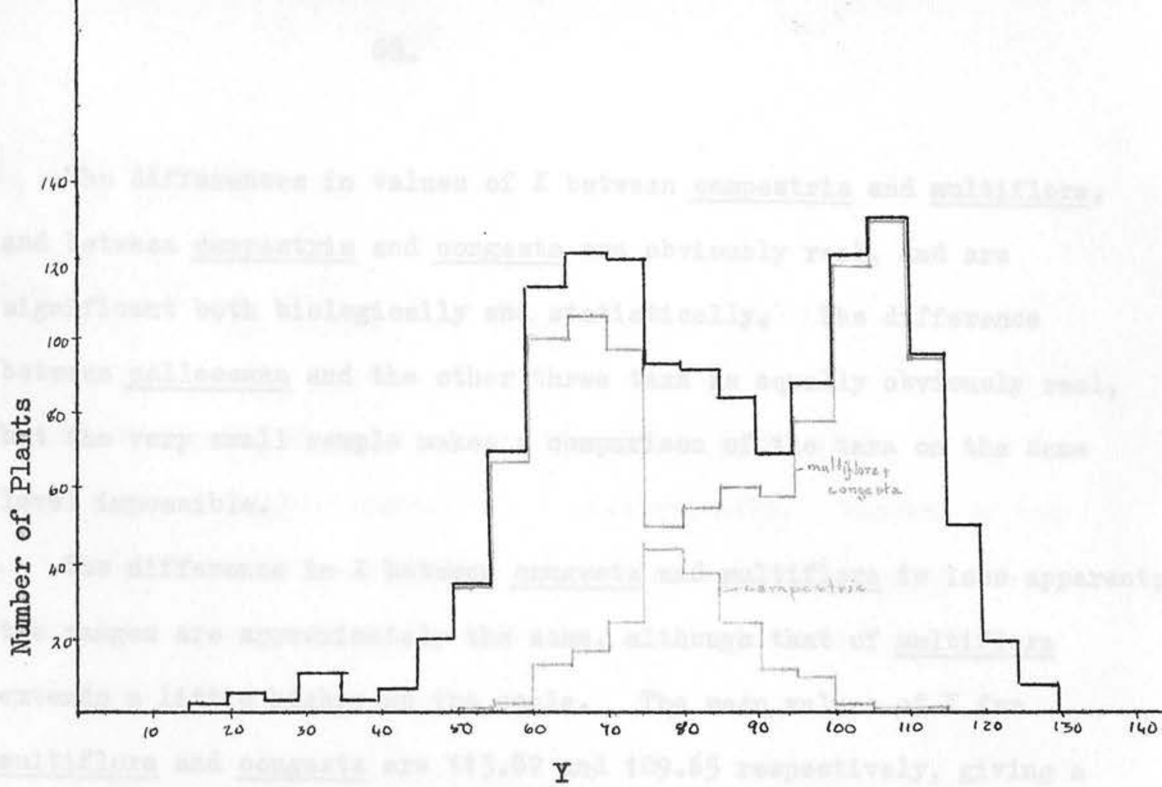


Fig. 33. Frequency histogram of the Y index.

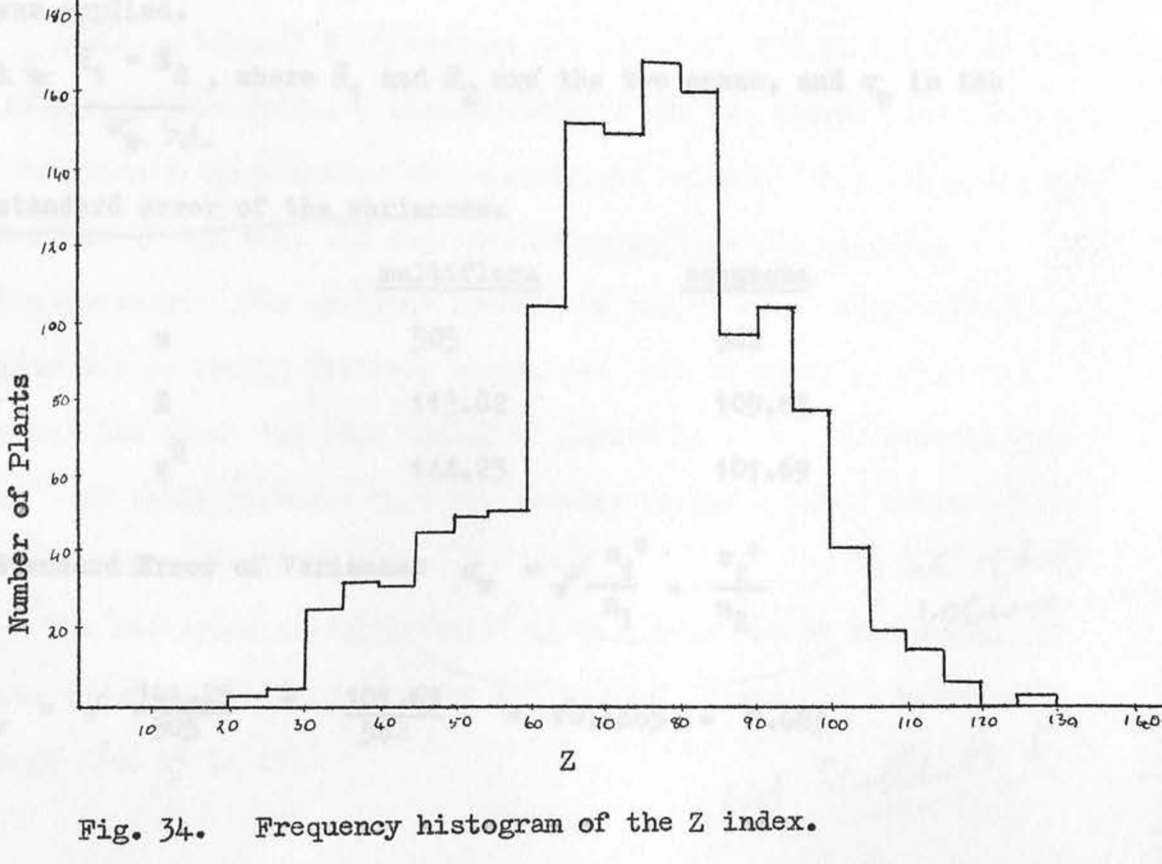


Fig. 34. Frequency histogram of the Z index.

The differences in values of X between campestris and multiflora, and between campestris and congesta are obviously real, and are significant both biologically and statistically. The difference between pallescens and the other three taxa is equally obviously real, but the very small sample makes a comparison of the taxa on the same level impossible.

The difference in X between congesta and multiflora is less apparent; the ranges are approximately the same, although that of multiflora extends a little higher up the scale. The mean values of X for multiflora and congesta are 113.82 and 109.65 respectively, giving a difference of 4.17 units.

To test the significance of this difference, Student's "t" test was applied.

$t = \frac{\bar{x}_1 - \bar{x}_2}{\sigma_w \; S_d}$, where $\bar{x}_1$ and $\bar{x}_2$ are the two means, and σ_w is the ~~standard error of the variances.~~

	multiflora	congesta
n	505	562
$\bar{x}$	113.82	109.65
s^2	144.25	101.69

Standard Error of Variances $\sigma_w = \sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}$ = S.E. of diff. between means

$$\sigma_w = \sqrt{\frac{144.25}{505} + \frac{101.69}{562}} = \sqrt{0.4665} = 0.683$$

Not Student's t

$$\bar{x}_1 - \bar{x}_2 = 4.17$$

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sigma_w} = \frac{4.17}{0.683} = 6.105 \quad P = < 0.001$$

Number of degrees of freedom = 505 + 562 - 2 = 1065

This result is highly significant - statistically. Whether or not it is significant biologically will be discussed later, when the individual characters of which the indices are composed are considered separately.

A frequency histogram was made for the Y index, using only those plants which had an X index of over 80 i.e. omitting all plants of campestris (fig. 33).

Again, a bimodal distribution was observed, but in this case there was a much less definite separation into the two groups, and there was a relatively large number of intermediate values. The two modes were at about 70 and 105, and represented multiflora and congesta respectively. The smallest numbers of plants were between 80 and 90; there was no really distinct break, and each category between these values had about the same number of plants in it - i.e. between 9 and 12. It seems probable that the overlap in the Y index between these taxa is of at least 10 units.

The histogram showed a "tail" at the lower end of the scale, and this consisted of the plants of pallescens; these had a value of Y range from 19 to 40.

The values of Y for campestris were also plotted on a frequency histogram; the distribution was more or less normal, and showed a mode at about 80, about mid-way between those of multiflora and congesta. (Fig. 33a).

The mean, variance and standard deviation of Y for the four taxa was worked out as for X.

In the case of multiflora and congesta, the intermediate values, i.e. those between 80 and 90 was arbitrarily divided between the two taxa. All values of 80 were considered as multiflora, all values of 90 as congesta, and the intermediate values were divided in such proportions that the majority of the plants with the higher values were taken as congesta, and the majority of the plants with the lower values were taken as multiflora. Although arbitrary, this method does allow a rather more accurate estimation of the ranges of multiflora and congesta than would be obtained by drawing the dividing line at 85, and allowing no overlap. The calculation of the variance and standard deviation is also made more accurate by this method.

From these results, (given in table 9) it is apparent that the mean values of multiflora (66.8) and congesta (104.1) differ by about 37 units. The difference between them is obviously significant, both biologically and statistically. Student's "t" was worked out as before, t equalling in this case 63.01; $P = < 0.001$.

When X and Y had been worked out, it was possible to separate the plants into four groups. The vegetative characters of these groups were then compared, using the Z index.

Histograms of Z for campestris, congesta and multiflora were constructed (fig. 44). These showed that campestris had the lowest values (i.e. it is the smallest), while multiflora and congesta were much larger. When the histograms of Z for congesta and multiflora were compared, the mode of congesta was at a slightly higher value than that of multiflora (Fig. 44a)

The histogram of Z for campestris is considerably skewed towards the lower end of the scale; this is probably because the use of $\sqrt{H}$ and $\sqrt{L}$ instead of H and L respectively is not sufficient to correct the skewness. However, when all three groups are taken together in one histogram, a fairly close approximation to a normal distribution is obtained, and a slight skewness in the distribution of Z for campestris seems to be unavoidable.

The mean, variance and standard deviation of Z for campestris, congesta and multiflora were worked out, as for X and Y; pallescens had to be omitted, as very few of the plants collected had stems taken right to the base, and several of them had had the leaves bitten off by animals.

Student's "t" test for Z, multiflora and congesta.

	congesta	multiflora
n	486	446
$\bar{x}$	82.12	74.29
s^2	231.45	162.61

$$\sigma_w = \sqrt{\frac{231.45}{486} + \frac{162.61}{446}} = \sqrt{0.8408} = 0.917$$

$$\bar{x}_1 - \bar{x}_2 = 82.12 - 74.29 = 7.83$$

$$t = \frac{7.83}{0.917} = 8.539 \; ; \; p = < 0.001$$

Number of Degrees of freedom = 486 + 446 - 2 = 932 - 2 = 930

This result is highly significant.

Student's "t" test for Z, campestris and multiflora.

	campestris	multiflora
n	152	446
$\bar{x}$	47.55	74.29
s^2	163.39	162.61

$$\sigma_w = \sqrt{\frac{163.39}{152} + \frac{162.61}{446}} = \sqrt{1.4396} = 1.1999 = 1.2$$

$$\bar{x}_1 - \bar{x}_2 = 26.74$$

$$t = \frac{26.74}{1.2} = 22.28 \; ; \; p = < 0.001$$

Number of degrees of freedom = 152 + 446 - 2 = 596

This result is highly significant.

The three indices were treated graphically by plotting two of them against each other in a scatter diagram. In fig. 35 X and Y are represented in such a diagram. The plants used to make up this diagram are all those which were collected in the mass gatherings and which were sufficiently complete to allow the indices to be calculated - a total of about 1,500 plants.

The diagram shows that the dots representing the plants form three areas of concentration, each of which corresponds to one of the three taxa, campestris, multiflora and congesta. Using the limits suggested by the histograms, the diagram can be divided into three areas, each containing one of the concentrations of dots, or one taxon. By working out X and Y for any given plant, and then plotting them on this graph, it is possible to find out to which of the taxa it belongs, or, if it appears to be intermediate, to which of them it is most closely allied. This information can, of course, be obtained by merely working out the indices, but results presented in a graphical manner are often more easily interpreted by a botanist than when they are presented as a table of numbers.

To further emphasise the concentrations of plants it is possible to "contour" the scatter diagram (fig. 36). Lines are drawn through areas of equal concentration of dots in the original scatter diagram (fig. 35). The mode for both indices for each taxon is indicated by the areas of greatest concentration, or "peaks". In this diagram the degree of separation of campestris from the other taxa is accentuated by the fact that there are fewer specimens of it than there are of the other two groups.

The indices may therefore be used to assign any given plant to one of the categories, but the system is far from being infallible. There must inevitably be a certain proportion of individuals which do not fall into any category. These may be of hybrid origin, or they be at the limit of variation of any or other of the taxa. On the other hand, over- or under-emphasis of one of the characters may have caused a distortion of the indices. For the vast majority of plants, however, the calculation of X and Y will give a clear indication of the taxon to which they belong, if this is not already obvious from the general appearance.

The characters of which the indices are composed are not all equally good for separating the taxa. In the following section methods of "weighting" the better characters will be discussed, and in particular, the use of the Discriminant Function.

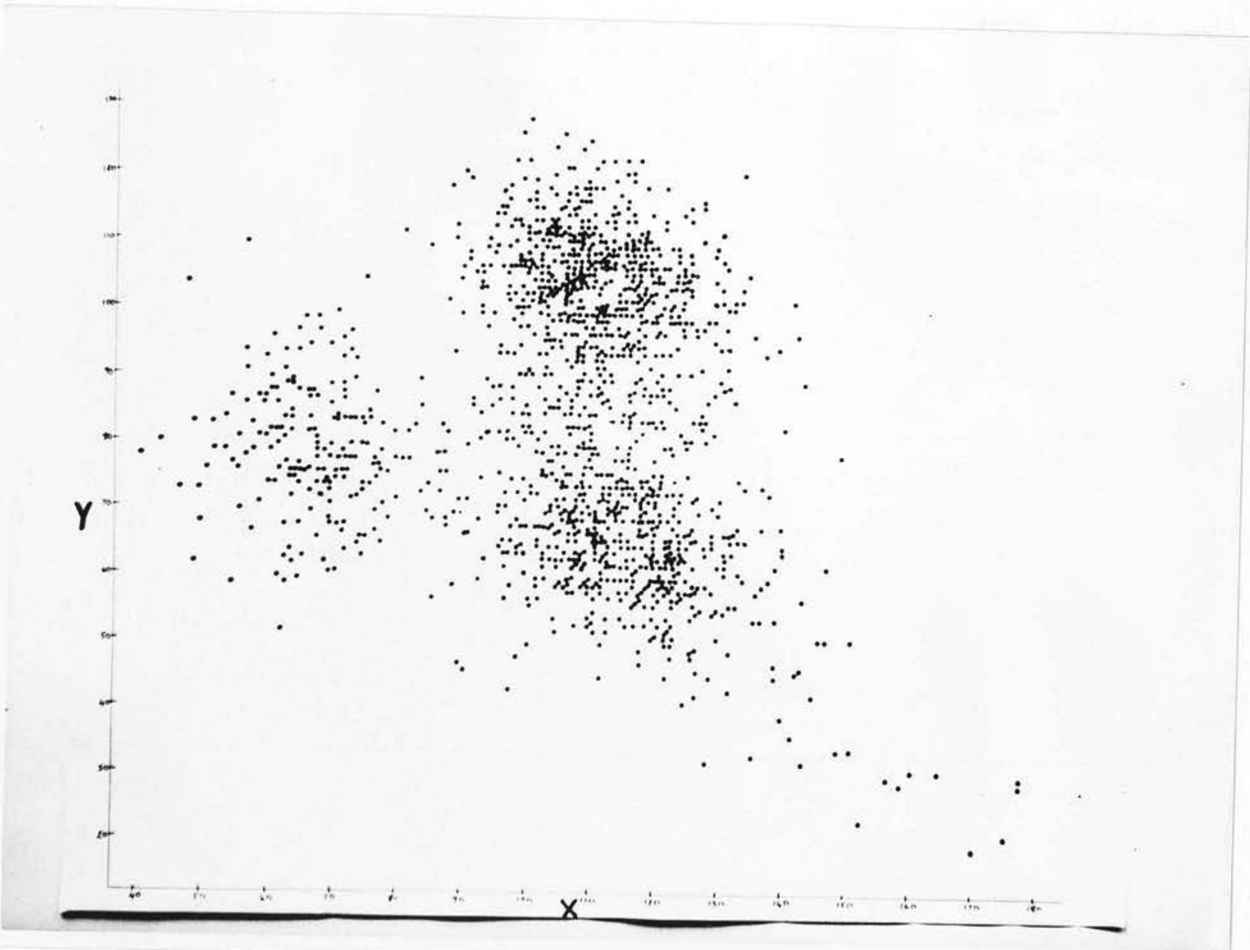


Fig. 35. Scatter diagram of X and Y.

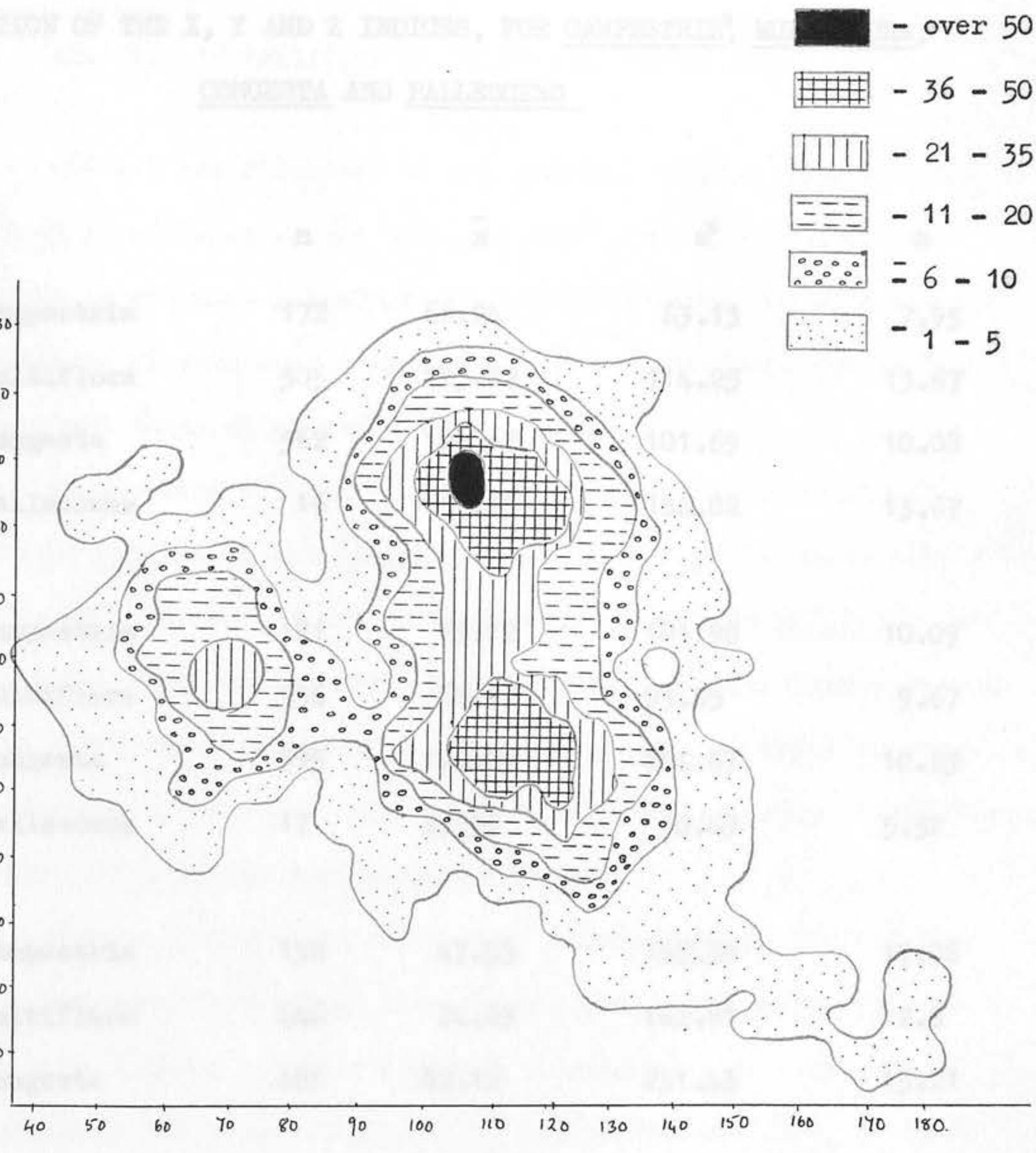


Fig. 36. Contoured diagram of fig. 35.

TABLE 9.

VARIATION OF THE X, Y AND Z INDICES, FOR CAMPESTRIS[2], MULTIFLORA, CONGESTA AND PALLESCENS

		n	$\bar{x}$	s^2	s
X	campestris	172	66.24	63.13	7.95
	multiflora	505	113.82	114.25	13.67
	congesta	562	109.65	101.69	10.08
	pallescens	16	156.75	186.82	13.67
Y	campestris	181	79.12	101.98	10.09
	multiflora	536	66.79	93.55	9.67
	congesta	595	104.09	104.67	10.23
	pallescens	17	29.59	30.49	5.52
Z	campestris	152	47.55	163.39	12.78
	multiflora	446	74.29	162.61	12.6
	congesta	486	82.12	231.45	15.21

F. ANALYSIS OF VARIATION IN INDIVIDUAL CHARACTERS.

The indices discussed in the previous chapter were used to effect a preliminary, and somewhat arbitrary, division of the plants in the mass gatherings into three groups; in this way the variation of each character used could be calculated for each of the three taxa, which could then be compared.

Plants with a value of X between 80 and 90 (intermediate between <u>multiflora</u> and <u>congesta</u> and <u>campestris</u>) and those with a value of Y between 80 and 90 (intermediate between <u>multiflora</u> and <u>congesta</u>) were omitted from the analysis, but were later compared with the results obtained to determine whether it might be possible to fit any of them into one or other of the categories on the basis of the value of one particular character.

Figure 37 shows the cumulative curves (ogives) derived from the measurements obtained from these plants, the curves for the three taxa being compared for each character. For the sake of simplicity the index values of the characters are used, so that they will all show positive correlations, and about the same range of variation will be shown by each character; decimals are also eliminated by this means. The characters will be considered separately, and the taxa compared in tabular form below.

Stem Height

	campestris		multiflora		congesta	
	index	cm.	index	cm.	index	cm.
max.	29	33	43	61	48	73
mean	18.1	16	28.9	33	32.1	38
min.	4	4	11	9	10	8
s	4.8		5.6		6.2	
s^2	23.3		31.7		38.4	
n	182		478		546	

The mean height of the stem in campestris is considerably less than that of the other two taxa, with a difference of over 10 units, or 17 cm., from that of multiflora, and of 14 units (22 cm.) from that of congesta. The difference in stem height of multiflora and congesta is statistically significant, but is hardly enough to use as a taxonomic character.

Leaf length

	campestris		multiflora		congesta	
	index	cm.	index	cm.	index	cm.
max.	36	14	47	22	47	22
mean	17.7	5	28.4	10	29.4	10.5
min.	7	2.3	13	4	12	3.5
s	6.1		5.8		6.5	
s^2	37.0		33.5		41.6	
n	152		433		481	

The leaf length shows a similar variation pattern to that of the stem height, the leaves of campestris having a mean value over 10 units lower than those of multiflora and congesta, which are separated by only one unit.

Leaf Width.

	campestris		multiflora		congesta	
	index	cm.	index	cm.	index	cm.
max.	22	0.34	29	0.44	41	0.61
mean	11.5	0.20	17.4	0.27	20.6	0.32
min.	3	0.08	5	0.11,	7	0.13
s	3.5		4.5		5.6	
s^2	12.6		19.9		31.3	
n	169		463		533	

The difference in the mean width of the leaf in campestris from that in multiflora is about 6 units, while the mean of multiflora is about three units less than that of congesta. These differences are significant statistically, but they are of little taxonomic use.

These three characters together make up the Z index, in which the mean value of campestris is 47.2, and differs highly significantly from those of congesta (82.5) and multiflora (74.9). The two latter means also differ significantly, the main difference arising from the greater stem height of congesta, although the other characters show a similar but lesser difference. The index of vegetative characters might be used taxonomically when comparing campestris with multiflora or congesta, and it is usually possible to distinguish this taxon from the other two even when there are no flowers available. The differences between multiflora and congesta are too small to be of use in this way.

Number of Flowers.

	campestris		multiflora		congesta	
	index	no.	index	no.	index	no.
max.	16	40	36	90	32	80
mean	7.5	15-20	15.1	35-40	12.4	30-35
min.	2	5	4	10	4	10
s	2.4		5.1		4.4	
s^2	5.6		25.8		19.8	
n	183		489		552	

The number of flowers in the inflorescence was counted to the nearest five, as it was difficult to prevent flowers dropping off when the plants were dried, which made accurate counting impossible.

The highest average number of flowers in the inflorescence is found in multiflora; congesta has rather fewer, and campestris has a much lower average number of flowers than either. The ogives of this character in fig. 37 show that the distribution is rather skewed, and the standard deviations increase with the increase in the mean value, so that it seems that this character should have been converted to index values of a square-root or a logarithmic scale. This would probably have emphasized the differences between campestris and the other taxa, and possibly have minimised the difference between the latter.

Number of Heads.

	campestris		multiflora		congesta	
	index	no.	index	no.	index	no.
max.	10	5	26	13	18	9
mean	6.2	3.1	10.8	5.4	8.6	4.3
min.	2	1	4	2	4	2
s	1.8		3.4		2.4	
s^2	3.2		11.4		5.7	
n	183		489		552	

The number of heads in the inflorescence varies in much the same way as the number of flowers, and it seems again that a square-root or a logarithmic scale would have been more appropriate, and would have corrected the skewed distribution shown in the ogives in fig. 37. This skewness is less obvious when individual populations are studied, than when they are all considered together.

The differences of the means are only two units each, but the maxima show greater differences, and multiflora is again the taxon with the highest value of the mean, congesta is intermediate, and campestris is the lowest.

<u>Stamen</u> <u>Length</u>.

	campestris		multiflora		congesta	
	index	mm.	index	mm.	index	mm.
max.	34	1.38	42	1.06	44	0.98
mean	23.8	1.8	33.4	1.4	31.9	1.46
min.	5	2.54	21	1.9	18	2.02
s	5.8		4.4		4.5	
s^2	33.3		19.7		20.5	
n	183		489		552	

In size of stamen <u>multiflora</u> and <u>congesta</u> have approximately the same mean, range and variance; <u>campestris</u>, on the other hand has a significantly lower index value, which corresponds to significantly larger stamens. The slight difference in the means of <u>congesta</u> and <u>multiflora</u> is significant.

<u>Anther:filament</u> <u>Ratio</u>.

	campestris		multiflora		congesta	
	index	ratio	index	ratio	index	ratio
max.	28	.522	43	.312	44	.298
mean	16.3	.690	29.8	.495	30.6	.49
min.	5	.844	17	.676	17	.676
s	4.0		5.1		4.7	
s^2	16.0		25.9		22.1	
n	183		489		552	

The range, mean and variance of <u>multiflora</u> and <u>congesta</u> are again more or less the same, but the mean of <u>campestris</u> is very much lower than that of either of the others, different from them by about 14 units.

Seed Length : Width Ratio.

	campestris		multiflora		congesta	
	index	ratio	index	ratio	index	ratio
max.	23	1.44	42	1.82	43	1.84
mean	12.02	1.22	25.9	1.5	26.4	1.51
min.	3	1.04	9	1.16	17	1.32
s	3.8		5.1		4.02	
s^2	14.5		26.04		16.1	
n	183		489		552	

Once again multiflora and congesta have very similar mean values but the ranges are different; the minimum value of multiflora is 8 units less than that of congesta, while the means and maxima are about the same. The variance of multiflora is correspondingly higher than that of congesta. The mean of campestris is about 14 units less than those of congesta and multiflora, giving approximately the same degree of divergence from them as did the previous character.

The three last characters exhibit considerable constancy, particularly in the similarity of multiflora and congesta, and in the degree of difference of these from campestris. They are obviously better taxonomic characters than the number of heads and the number of flowers in the inflorescence; they might, however, have been used to better advantage had they been converted to a square-root or logarithmic scale, and had the number of flowers been counted more accurately. This would have involved pulling the whole inflorescence to pieces, and would have resulted in the destruction of the specimen, as well as being a very time-consuming process when applied to a sample of this size. The inclusion of pallescens in the range of variation for conversion to the index resulted in a considerable extension of the upper part of the range.

The difference in mean value of the X index for congesta and multiflora is seen from this analysis to be caused by the differences in the number of heads and of flowers in the inflorescence, since multiflora has an average of five heads and 35 to 40 flowers in the inflorescence, while congesta has an average of four heads and 30 - 35 flowers in the inflorescence.

The values of all five characters for campestris are significantly lower than they are for multiflora and congesta, so that the resulting index should be quite reliable in determining whether or not a plant is campestris.

Congestion Index.

	campestris		multiflora		congesta	
	index	cm.	index	cm.	index	cm.
max.	41	0.199	33	0.35	49	0.115
mean	21.6	0.79	17.6	1.0	39.4	0.22
min.	10	1.7	3	2.75	14	1.3
s	6.6		5.3		5.6	
s^2	43		28		31.2	
n	181		489		552	

The means of multiflora and congesta differ by about 22 units, and are 17.6 and 39.4 respectively. The amount of overlap is considerable, despite this difference, and is caused mainly by the "tail" of the congesta group, which has a rather skewed distribution. This tail extends beyond the lower limit of the group which would be expected from the mean and standard deviation. The mean is 39.4, standard deviation is 5.6, and the estimated lower limit would be 39.4 - 5.6 x 3, which is 22.6; the lower limit is in fact 14. The upper and lower limits of the multiflora group are more or less as would be expected from the mean and standard deviation, and the distribution is normal (see fig. 37). Some of the plants in the congesta group with low values of the congestion index may in fact be multiflora which have been forced into the wrong category by the inadequacies of the index method, but these will be discussed later.

Campestris occupies a position intermediate between the other taxa, but it is nearer to multiflora, as might be expected, since it has a lax inflorescence, but with fewer heads on shorter stalks.

Seed Size.

	campestris		multiflora		congesta	
	index	size	index	size	index	size
max	40	152	36	140	47	173
mean	25.1	107	22.6	100	32.2	128
min.	9	59	5	47	18	86
s	5.4		4.7		5.04	
s^2	29.4		22.5		25.4	
n	183		489		552	

The seeds of congesta are considerably larger than those of multiflora; the difference between the mean is 10 units, only about half the difference between the means of the congestion index, but still significant.

The position occupied by campestris is again intermediate, but the seeds are nearer the size of multiflora than of congesta.

Perianth Size.

	campestris		multiflora		congesta	
	index	mm.	index	mm.	index	mm.
max.	49	4.28	37	3.56	49	4.28
mean	32.4	3.3	24.8	2.8	33.8	3.35
min.	21	2.60	10	1.94	20	2.54
s	5.5		4.5		5.2	
s^2	29.7		20.5		26.9	
n	183		489		552	

The size of the perianth in multiflora and congesta shows a similar relationship to the seed size in these groups; congesta has a mean 9 units greater than that of multiflora, and a slightly higher variance. In this character, however, campestris is much nearer to congesta than it is to multiflora, having rather large perianth segments.

The index which is calculated from these measurement, Y, can be used to separate congesta and multiflora with a fair degree of accuracy, but there are some plants in the congesta group (Y greater than 90) which have a congestion index abnormally low for that taxon, but typical of multiflora. The values of the seed and perianth sizes of some of these

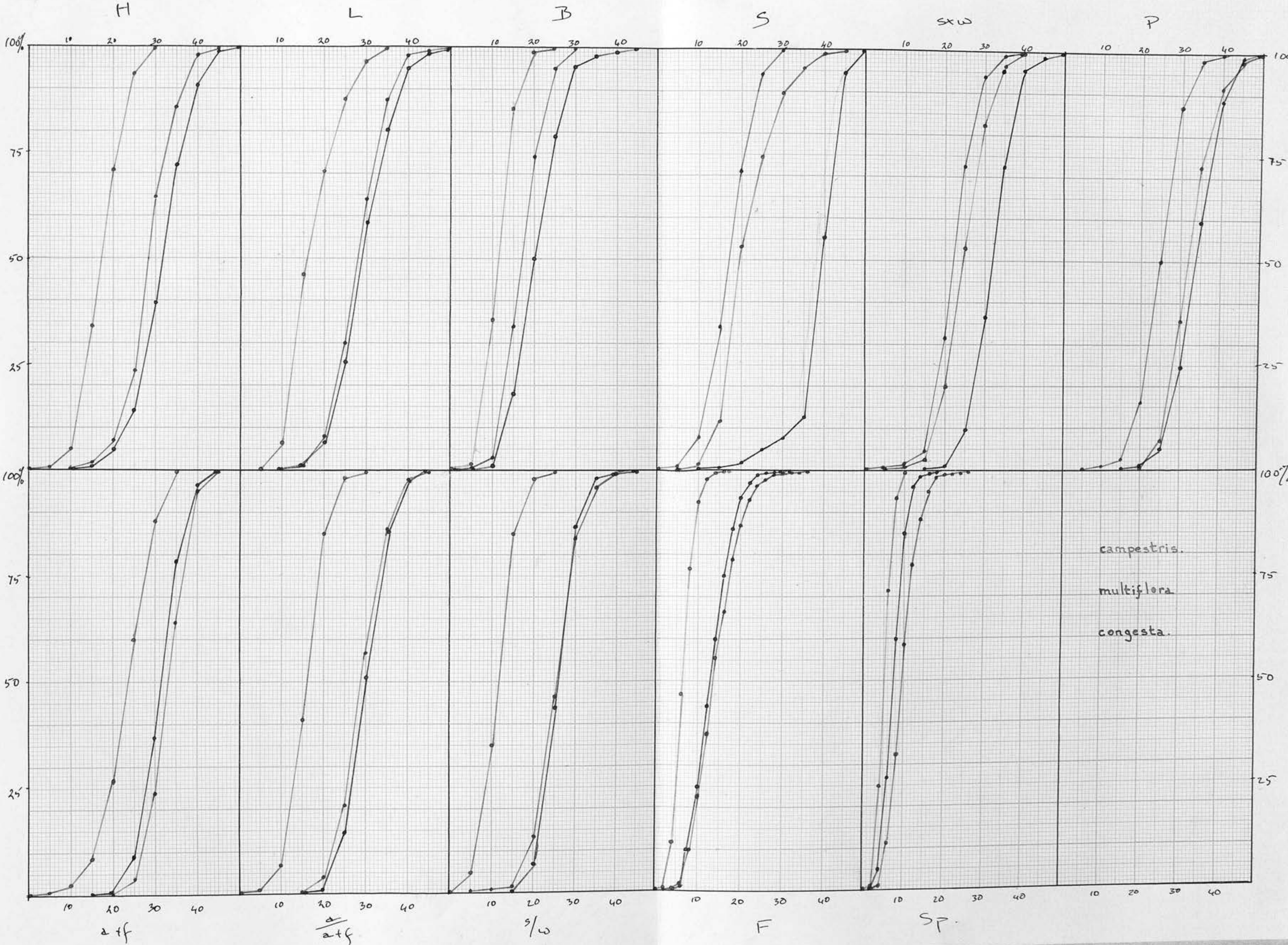


Fig. 37. Ogives of the diagnostic characters of campestris, multiflora and congesta.

plants are within the range of these characters for multiflora, and it seems that these individuals would be more correctly included in that taxon. The remainder, if included with multiflora would extend the range of variation of the seed or perianth size, and it seems unwise to include them in that group.

Part of the confusion may lie in the method of calculating the congestion index; this is the mean length of the spikelet stalks in the inflorescence. If an inflorescence has five heads more or less sessile, and one stalked, then the value of the congestion index will depend on the length of that stalk: if it is only about 1 cm. long, the congestion index may fall within the normal range for congesta, or only just outside it. On the other hand, the stalk may be 3 or 4 cm. long, which will very much increase the congestion index, and will probably bring it within the range of multiflora in that character. The question then is, are these plants multiflora or congesta, or are they possibly hybrids between the two? Evidence from cultivated plants, which will be discussed later, indicates that it is probable that some of these plants are in fact hybrids, while others may be congesta. The ~~true~~ status of these plants cannot be determined without a chromosome count, unless the nature of the congested inflorescence is properly understood. The latter will involve a long-term programme of crossing and back-crossing of multiflora and congesta, and the former is not possible once a specimen has been dried.

It appears that the best method of treating these plants with a low value for the congestion index (multiflora) and a high value for seed and perianth size (congesta)is to consider tham as possible hybrids between the two, until experimental work can throw more light on their true nature.

All plants having values of X between 80 and 90, and of Y between 80 and 90 were omitted from the above calculations. There were thirty plants in the first group; a histogram of X for these plants is skewed towards the upper end, and indicates that the plants are probably nearer to multiflora and congesta than they are to campestris.

The ranges of stamen size, anther:filament and seed length:width ratios are all within the ranges of these characters for multiflora and congesta, although in the lower part, where they overlap with campestris. The number of heads and of flowers in the inflorescence are also in the lower part of the range of multiflora and congesta, (fig. 39). From this evidence it seems best to treat all plants with a value of 81 or over as multiflora or congesta, and those with a value of 80 or less as campestris. A few errors might be made this way, but a very high proportion of the identifications would be correct.

When a histogram is made of Y, two groups of plants are seen (fig.40). Most of these have a value of Y less than 90, and can be considered as multiflora; eight plants have a value of Y over 100, and a congestion index of over 30, and can be considered as congesta.

The thirty plants which appeared to be intermediate between campestris and the other taxa can therefore be divided between them, in the ratio 22 multiflora and 8 congesta.

The second group of doubtful plants, intermediate between *multiflora* and *congesta*, can be treated in a similar manner. A histogram of Y shows a more or less even distribution of the values from 80 to 90 (fig. 41). A histogram of the congestion index shows a bimodal distribution, so that the plants can be divided into two groups, with lax or congested inflorescences. Where the other characters, seed and perianth size, fall within the range of these characters as shown in the ogives in fig. 37, they are referred to either *congesta* or *multiflora* on the basis of the congestion index. This allows most of the plants to be assigned to one or other of the categories. The remainder join those plants with a value of Y over 90, but with a congestion index of less than 30, in the group of putative hybrids.

The principal use of the indices is not so much to identify the plants, as to provide a basis for the initial separation of the plants into groups. Subsequent analysis of the variation of individual characters may modify this division, and possibly correct some errors, and it may be possible to assign plants with intermediate values of the index to one or other of the taxa.

Figures 42, 43 and 44 show the amended histograms of X, Y and Z for *campestris*, *multiflora* and *congesta*; the group of putative hybrids is omitted, and ~~are~~ is given separately in figure 45.

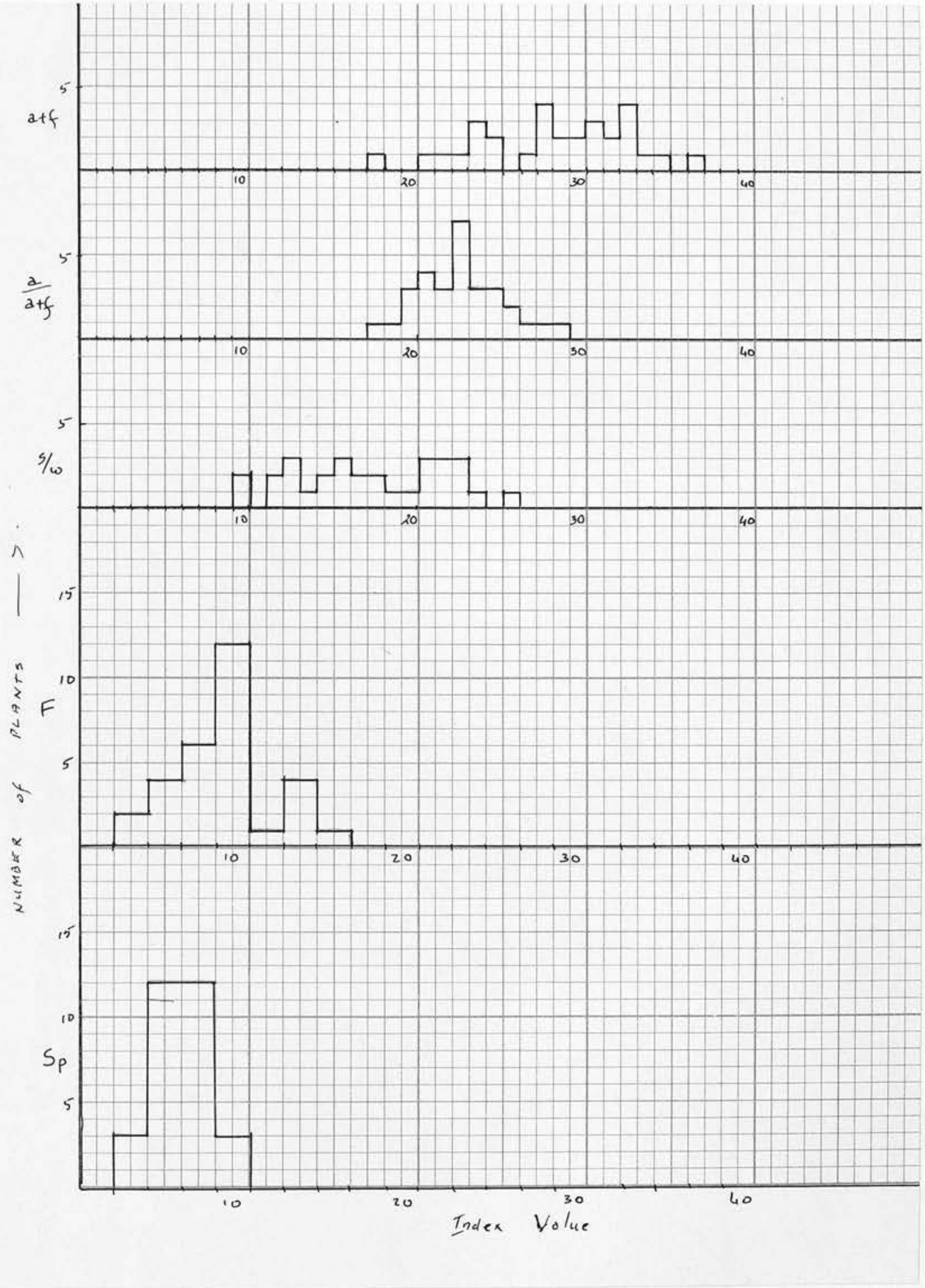


Fig. 39. Frequency histograms of a + f, $\frac{a}{a + f}$, s/w, F and Sp for the plants with X between 80 and 90.

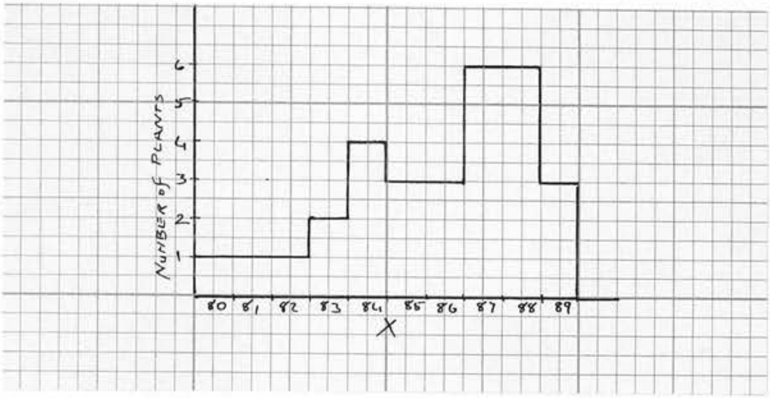


Fig. 38. Freuqency histogram of X between the values of 80 and 90.

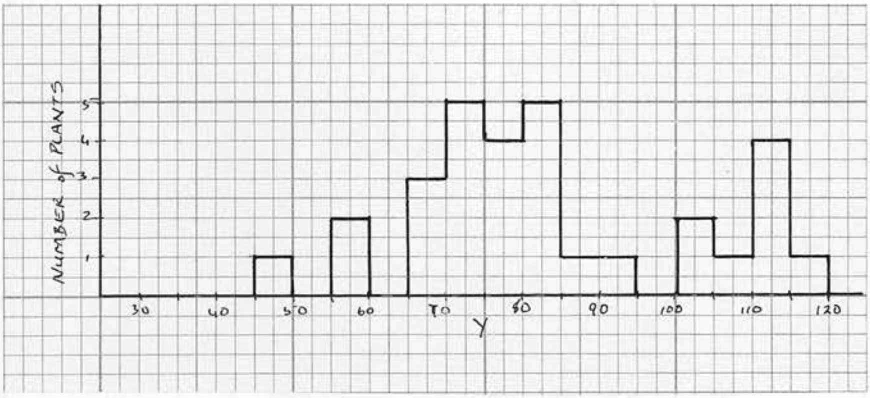


Fig. 40. Frequency histogram of Y, where X = 80 - 90.

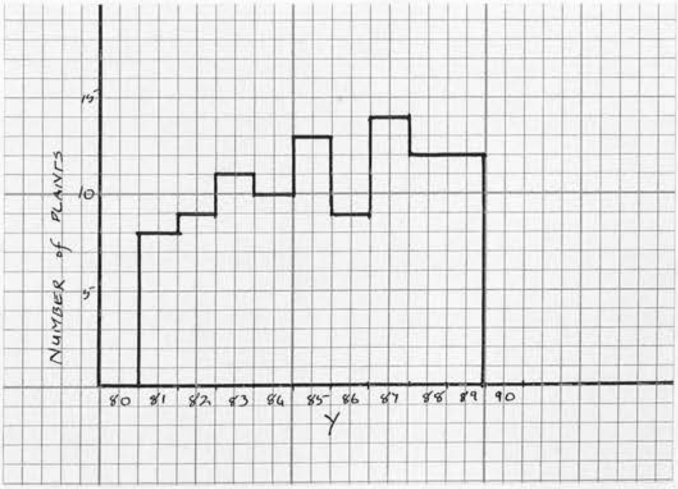


Fig. 41. Frequency histogram of Y between the values of 80 and 90.

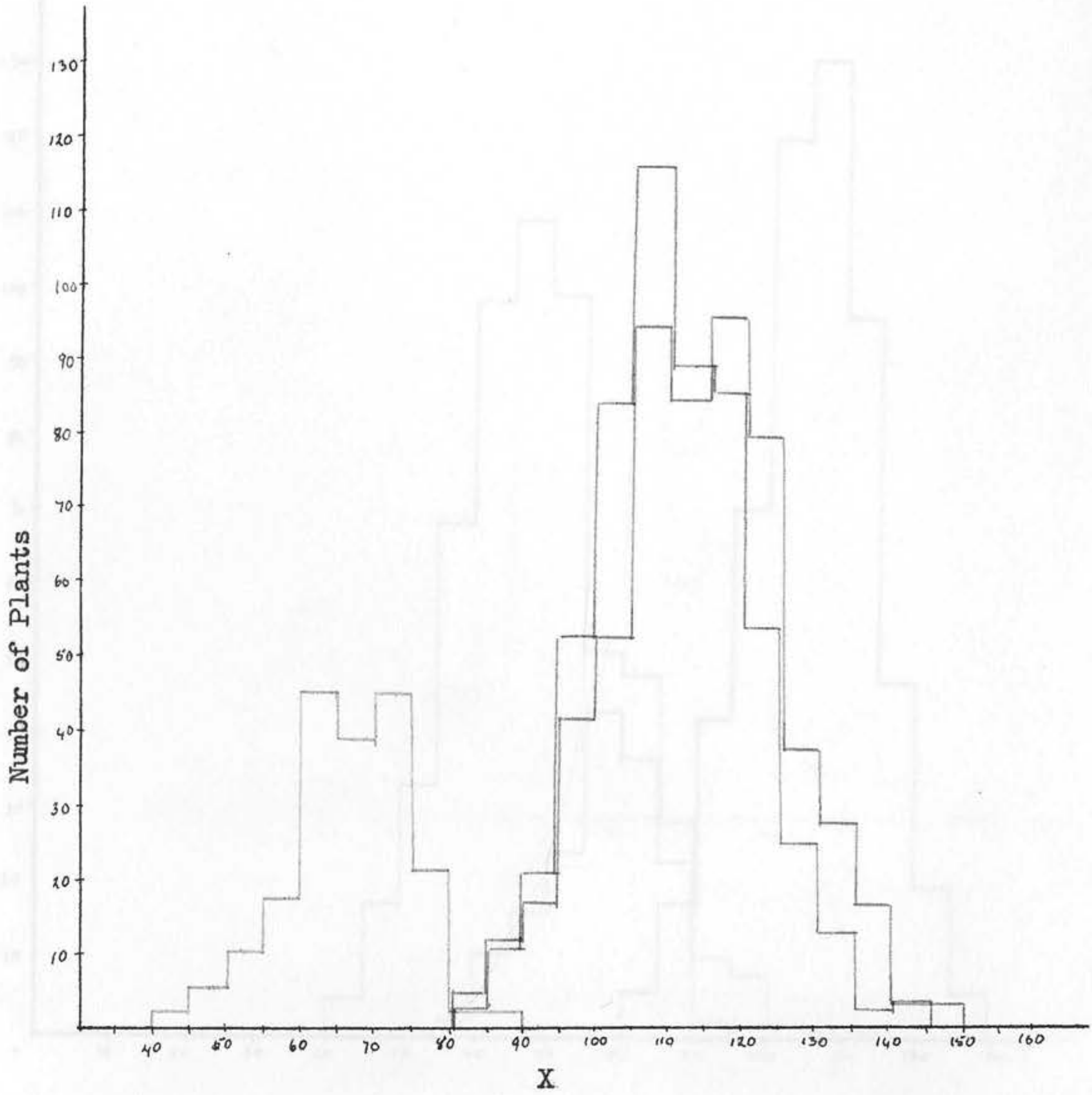


Fig. 42. Frequency histograms of the X index for campestris (green), multiflora (red) and congesta (blue).

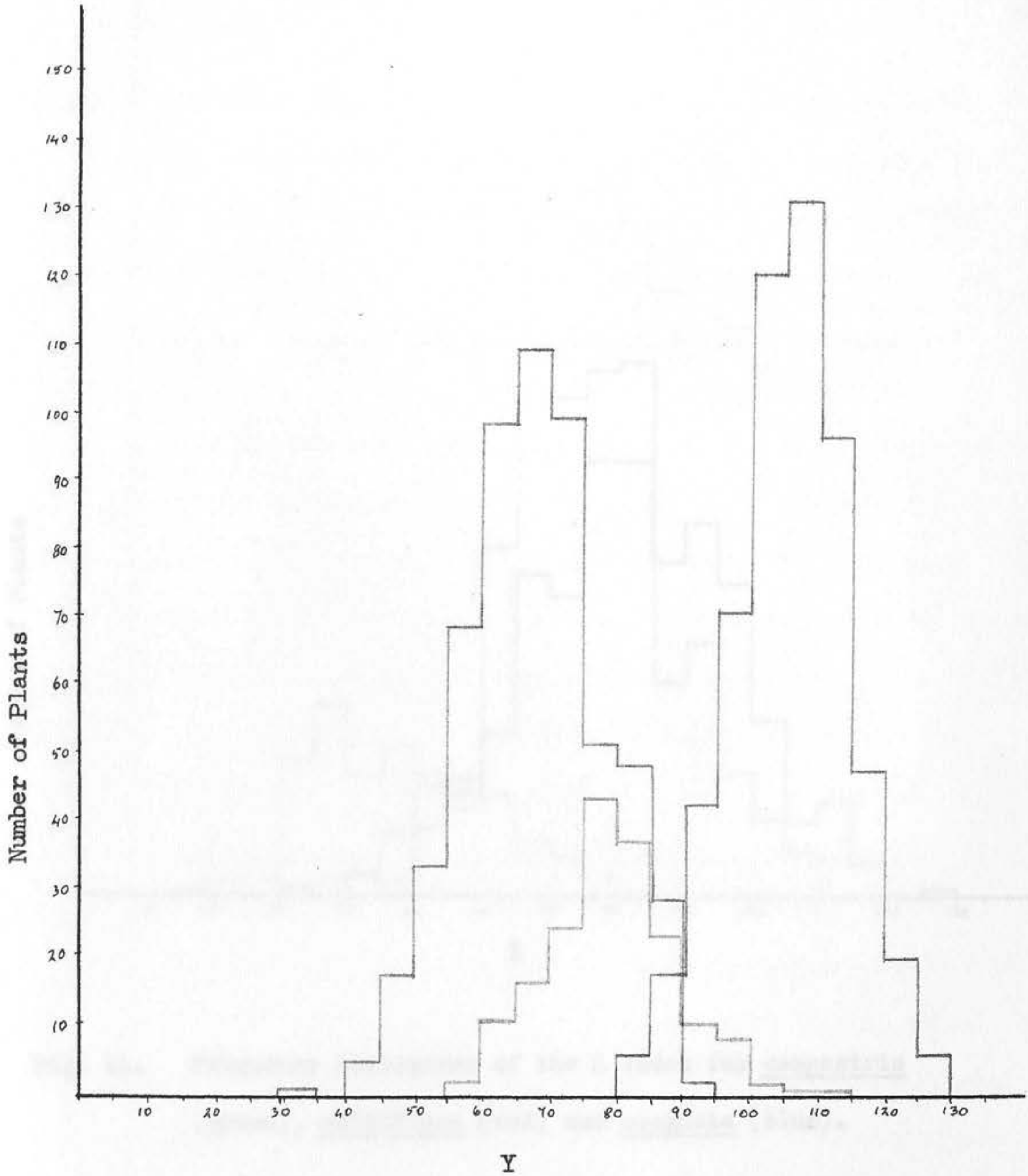


Fig. 43. Frequency histograms of the Y index for <u>campestris</u> (green), <u>multiflora</u> (red) and <u>congesta</u> (blue).

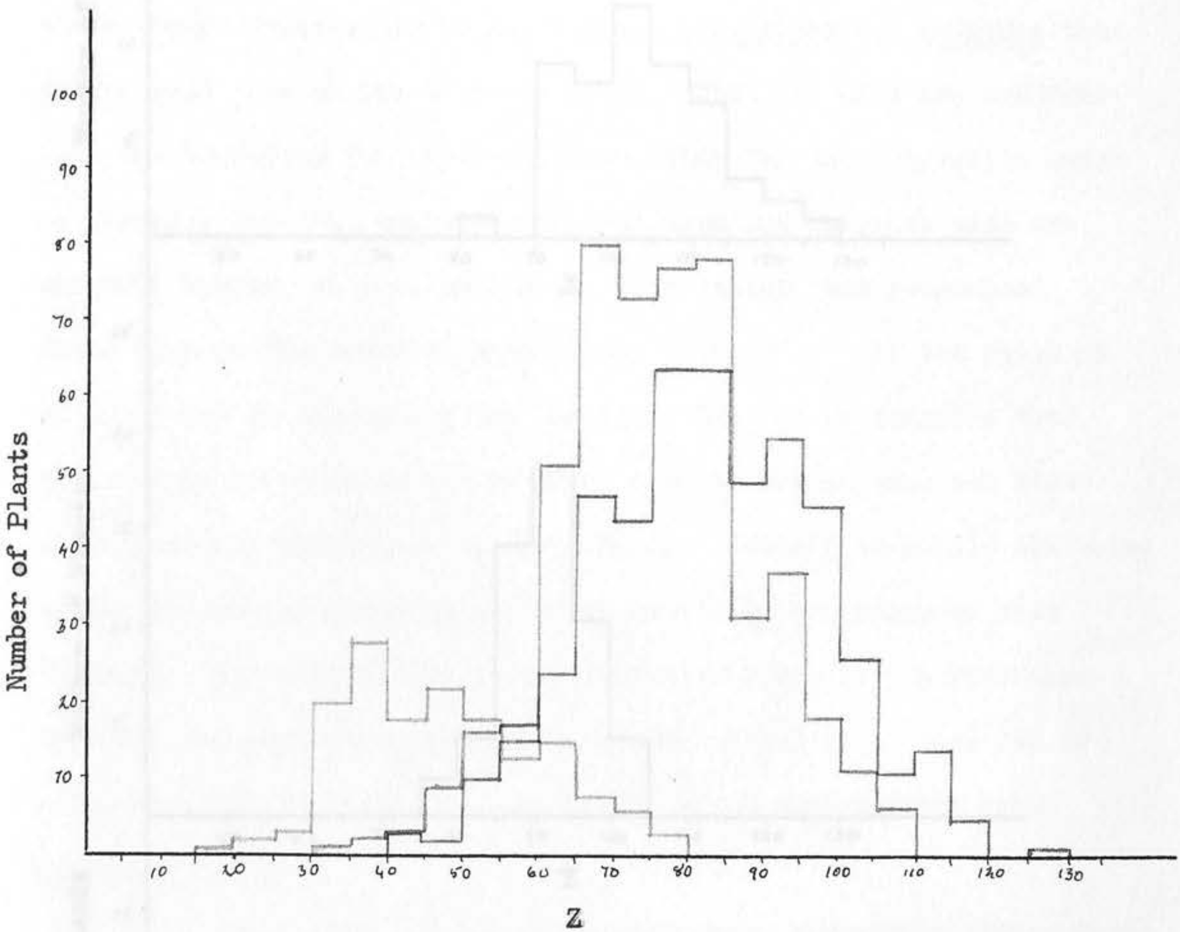


Fig. 44. Frequency histograms of the Z index for campestris (green), multiflora (red) and congesta (blue).

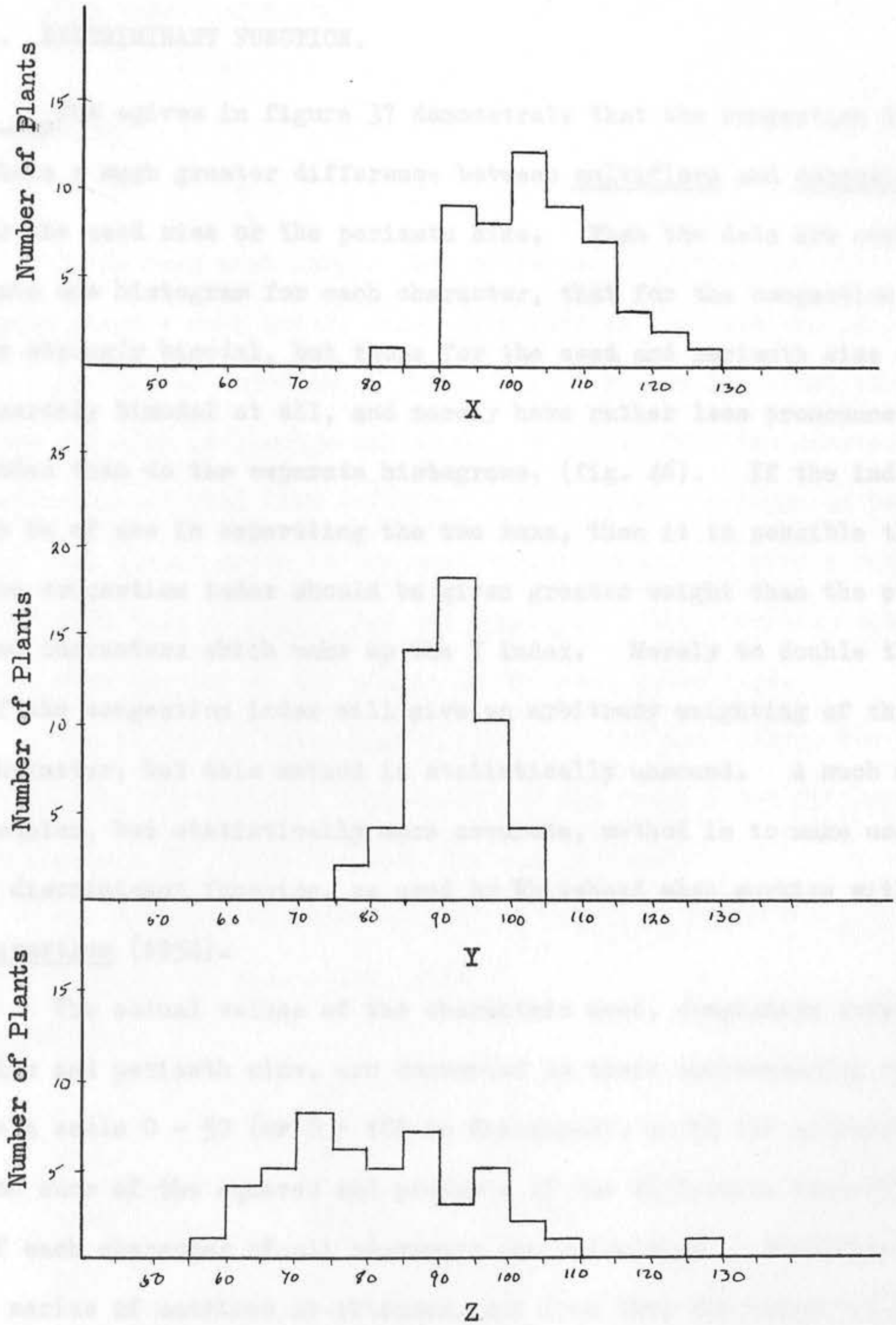


Fig. 45. Frequency histograms of the X, Y and Z indices of the putative hybrids between multiflora and congeata.

G. DISCRIMINANT FUNCTION.

The ogives in figure 37 demonstrate that the congestion index shows a mugh greater difference between multiflora and congesta than do the seed size or the perianth size. When the data are combined into one histogram for each character, that for the congestion index is strongly bimodal, but those for the seed and perianth size are scarcely bimodal at all, and merely have rather less pronounced modes than do the separate histograms, (fig. 46). If the index is to be of use in separating the two taxa, then it is possible that the congestion index should be given greater weight than the other two characters which make up the Y index. Merely to double the value of the congestion index will give an arbitrary weighting of that character, but this method is statistically unsound. A much more complex, but statistically more accurate, method is to make use of a discriminant function, as used by Whitehead when working with Cerastium (1954).

The actual values of the characters used, congestion index, seed size and perianth size, are converted to their corresponding values on a scale 0 - 50 (or 0 - 100 in Whitehead), as in the calculation of Y. The sums of the squares and products of the difference from the mean of each character of all specimens are calculated. From these results a series of matrices is obtained, and from them the values of F (the discriminant function) are obtained. The corrected index is then obtained by multiplying the congestion index by F_1, the seed size by F_2 and the perianth size by F_3.

The values of F are

$F_1 = 15$

$F_2 = 2$

$F_3 = 6$

F_1 is very much larger than either F_2 or F_3 because the congestion index gives a much better separation than do the seed and perianth size.

For the calculation of the values of F material other than that from the mass gatherings was used. This was from two sources (i) herbarium material from Britain, to give as wide a range as possible, and (ii) plants grown in the experimental garden to give a total of 50 plants each of _multiflora_ and _congesta_. The resulting discriminants were then applied to the plants in the mass gatherings.

The tables of the original values of the characters, the original index (Y), the weighted characters and the final index (Y') are given in Appendix II[2], together with the calculations.

The maximum, minimum and mean of the two indices for _multiflora_ and _congesta_ are summarised below.

MULTIFLORA.

	Y	Y'
max.	81	518
mean	57.76	367.88
min.	38	228
range	43	290

CONGESTA.

	Y	Y'
max.	116	960
mean	97.60	823.58
min.	75	515
range	41	445

The range of Y for <u>multiflora</u> and <u>congesta</u> is about the same number of units, 43 and 41 respectively, but the range of Y' is much greater for <u>congesta</u> than it is for <u>multiflora</u>, and the curve is skewed so that the mean is far nearer the maximum than it is to the minimum. This skewness is caused by the presence in the lower part of the range of two plants with values of Y equalling 88 and 75, and of Y' 621 and 515 respectively. The second of these seems certainly to come within the <u>multiflora</u> group, although at the extreme upper limit of it, while the first occupies a more doubtful position.

The histograms in fig. 47 show the distribution of Y in the two groups of plants, showing a slight overlap. Figure 48 is of the index with the discriminant function applied, and displays the division into two distinct groups, with a single more or less intermediate plant (Y' = 621); the plant with Y' = 515 comes into the <u>multiflora</u> histogram.

The total range of variation of Y is 38 to 116, 78 units, while that of Y' is 228 to 960, 732 units. The range of Y' is therefore about 10 times that of Y, so that the class intervals for the histograms of Y' are ten times those of Y, in this case 40 and 4 units respectively.

The discriminant function was then applied to the mass gatherings, and the resulting histogram (fig. 49) can be compared to that for Y (fig. 33). The separation into two groups is almost complete, and the considerable group of intermediate plants has been split between multiflora and congesta. The histogram of Y' resembles more closely that of the congestion index (fig. 46) than it does that of Y, which is to be expected, since that character receives more than twice the weight of either of the others.

The fact that Y' follows so closely the pattern of the congestion index leads one to consider again the utility of any type of index, when a single character can give an equally good, or even better, division into two groups. In this particular case, if ones principal aim is to separate one group of plants from another, it is obviously more simple to do so using the one good character, the degree of congestion of the inflorescence, than to go to the trouble of measuring three characters, converting the measurements to index values, which are then multiplied by the appropriate factor and finally added together to give an index. In addition, the degree of congestion of the index can usually be assessed at a glance, where all the heads are more or less sessile (congesta) or lax (multiflora); in the cases where there is one lax head and the rest are sessile, the congestion index may have to be worked out more accurately, but these plants should perhaps be treated as possible hybrids in any case.

Figure 51 is a scatter diagram of Y and the congestion index (S) of the plants used to calculate the discriminant function. Both give a separation of the plants into two groups, but S gives a more clear-cut division than Y. The _congesta_ and _multiflora_ groups are quite separate; one plant appears to come in an intermediate position between the groups, and one of the original _congesta_ plants comes within the _multiflora_ group. There is little or no correlation of the two characters within the groups, although they show a positive correlation when combined.

Figure 52 is a scatter diagram of Y' and the congestion index. The division into two groups is again very apparent, and there is a strong positive correlation both within and between the groups, which would be expected from the great weight given to S in the calculation of Y'. If the plants were separated on the congestion index only, the division would be much the same as if Y' were used; the only plant which would occupy a somewhat different position would be the one with an intermediate value of Y', which would be included with _multiflora_. In this series of plants it seems that only one possible error might be made if S were used instead of Y or Y', and the effect was to push an intermediate plant into the category to which it was closest in the index.

That one character alone is insufficient to separate two groups of plants into species is an established taxonomic principle. The previous sections have shown that _multiflora_ and _congesta_ are separated quite clearly by one character, the degree of congestion of the inflorescence. This in itself might not be enough to be taxonomically important, but the character is correlated with two others, seed size and perianth size, which do not by themselves separate the plants into two groups. When all three characters are combined to give a simple index

(Y), the separation is much less good than then S is used alone. When S is given extra weight in the index, by the application of a discriminant function (Y'), the division is much better than with Y, and very closely resembles that given by S. It seems that the use of an index at all in this case is limited, if the sole object is to separate the plants into two groups; the use of S alone given by far the smallest number of intermediate forms.

The real problem seems to be not how to separate the taxa, but whether the separation shown by S is as real as it appears to be, and whether the proportion of intermediate forms shown by Y is not in fact closer to reality than the sharp division into two groups. If these plants are truly intermediate, and are of hybrid origin, then the use of the simple Y index seems to be the most appropriate. If the plants are not of hybrid origin, but have an intermediate value of Y solely because of the overlapping of the ranges of variation of seed size and of perianth size, then the use of S alone seems best to separate them. Cytological evidence, which will be discussed in the next chapter, indicates that the former approach will give rise to fewer errors.

From a practical point of view, the division of the taxa by the congestion index alone is sufficient in most cases, but from the theoretical point of view of deciding the relationships of the taxa, and their taxonomic status, it is necessary to consider all the associated characters. The use of the discriminant function seems, in this case, to be of little practical or theoretical value. It does not give as good a separation into two groups as the congestion

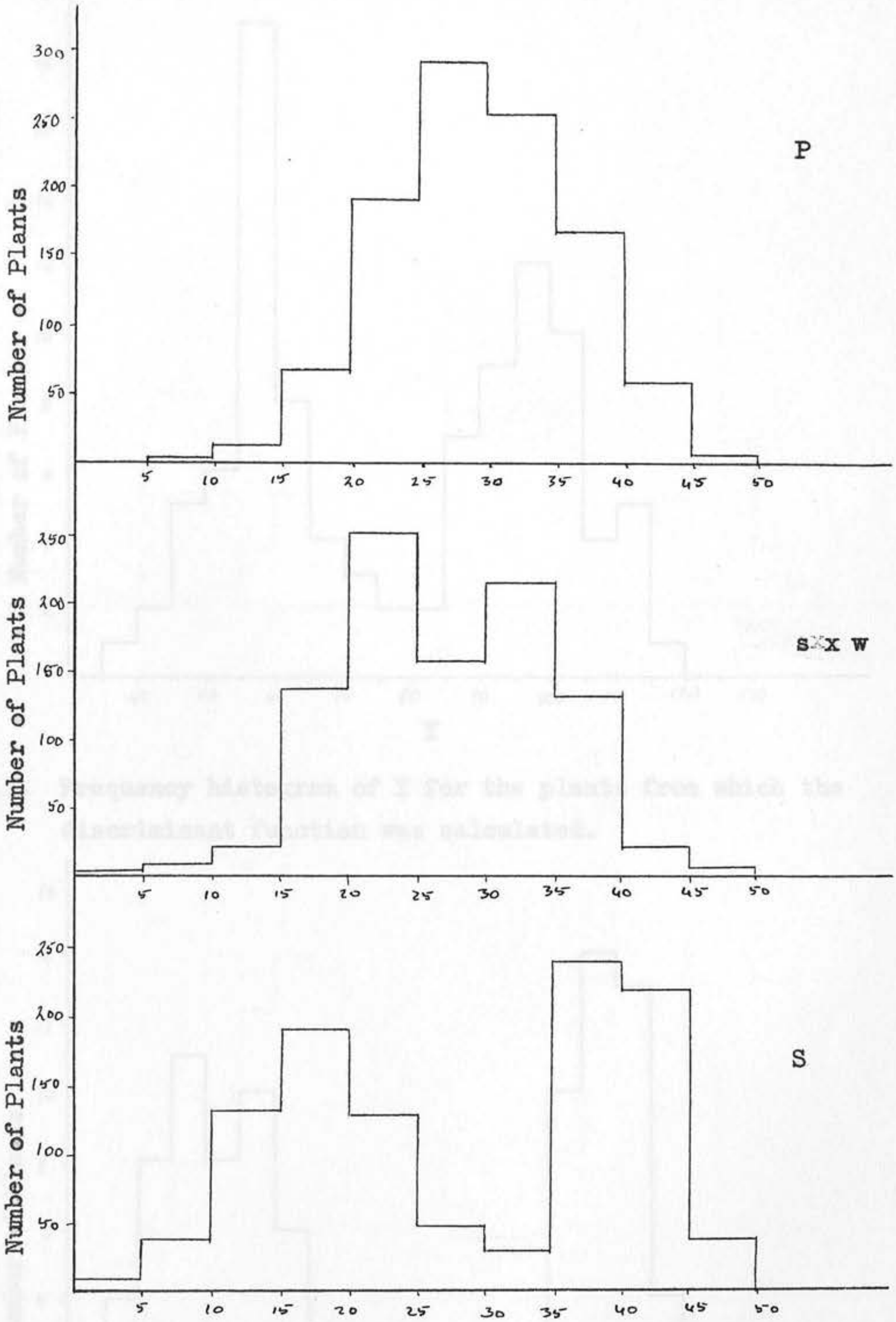


Fig. 46. Frequency histograms of the index values of S, s x w and P, for multiflora and congesta together.

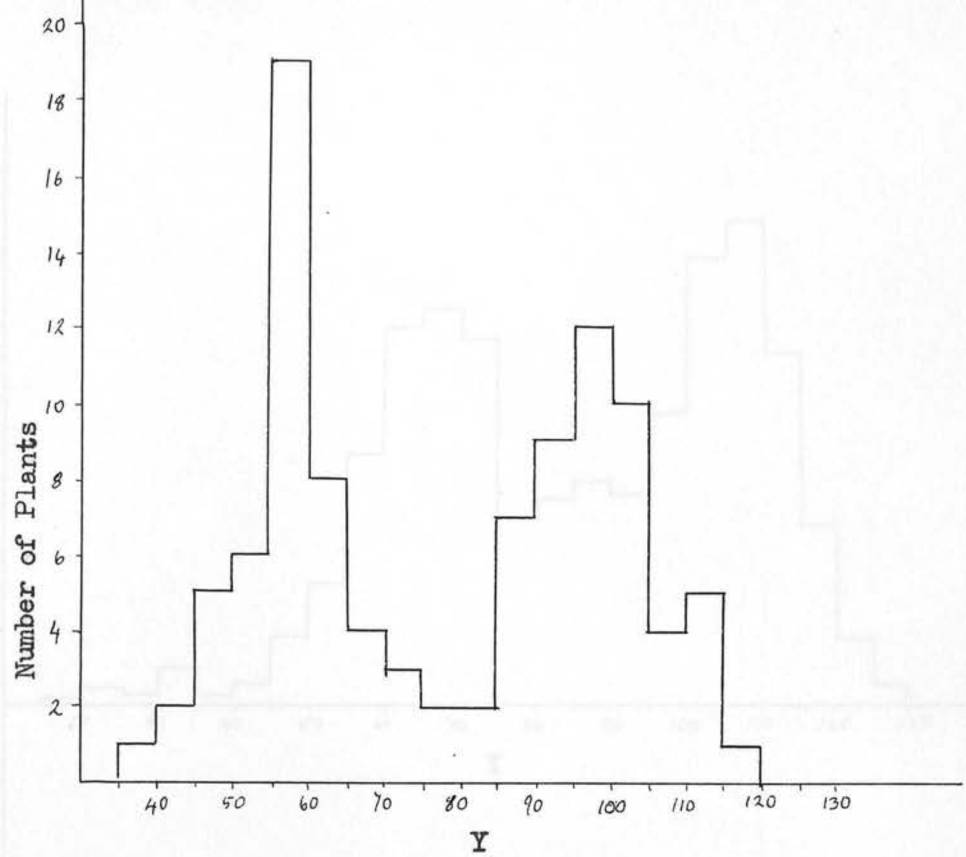


Fig. 47. Frequency histogram of Y for the plants from which the discriminant function was calculated.

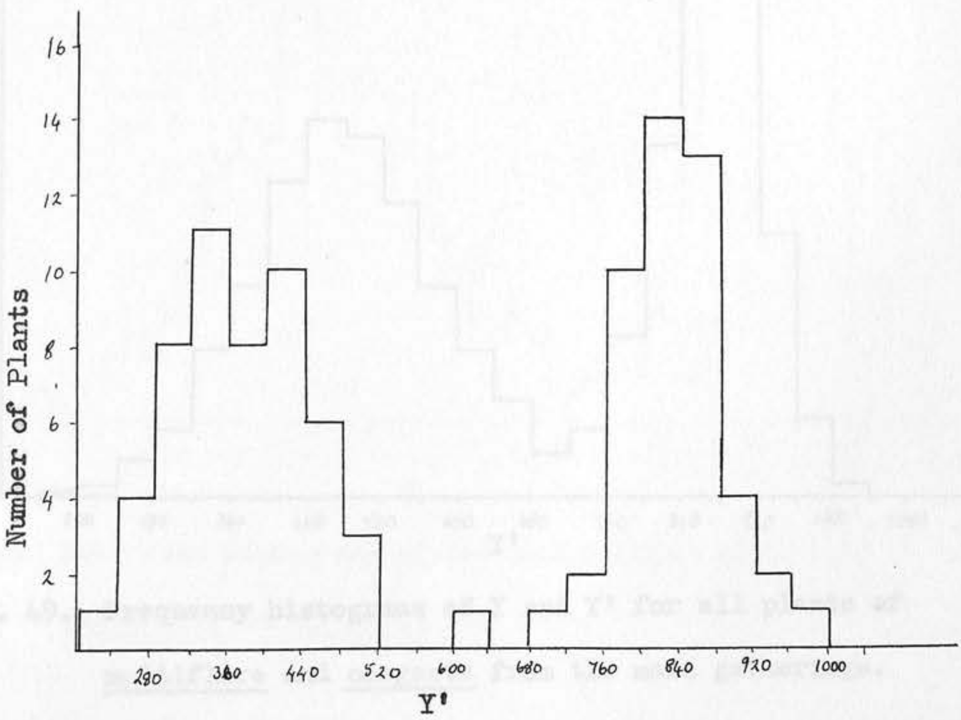


Fig. 48. Frequency histogram of Y' for the same plants as fig. 47.

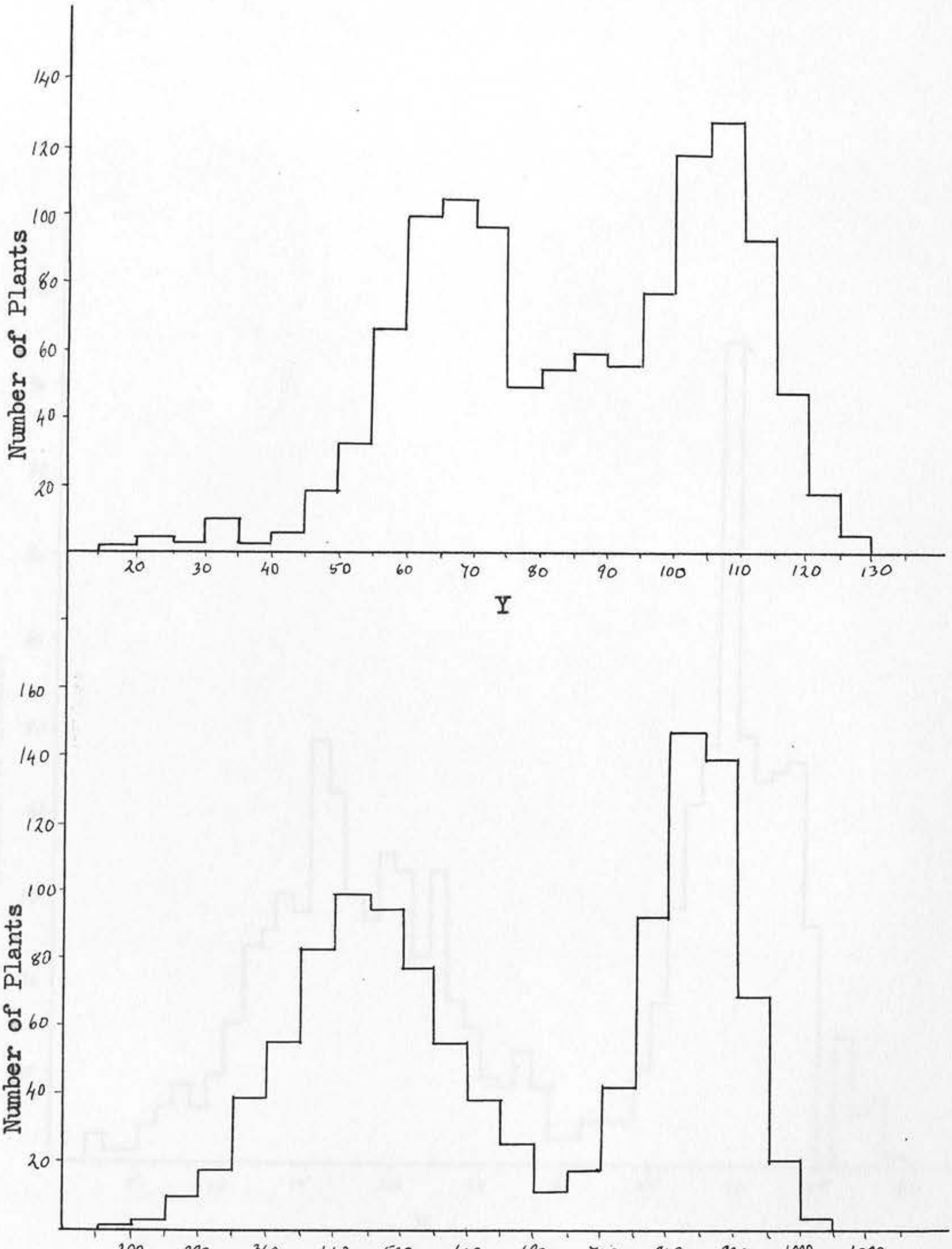


Fig. 49. Frequency histograms of Y and Y' for all plants of <u>multiflora</u> and <u>congesta</u> from the mass gatherings.

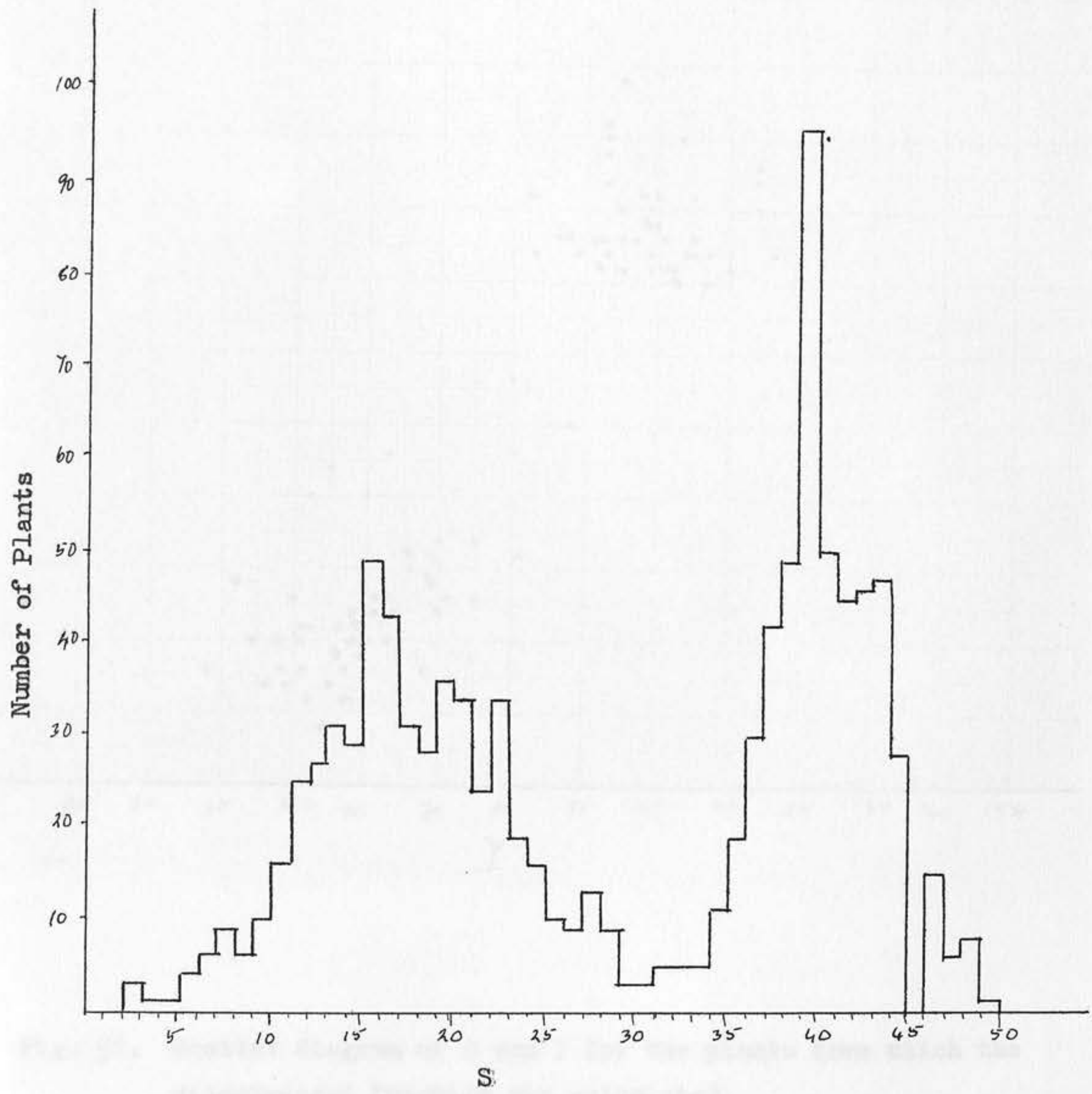


Fig. 50. Frequency histograms of the index values of S, for multiflora and congesta together.

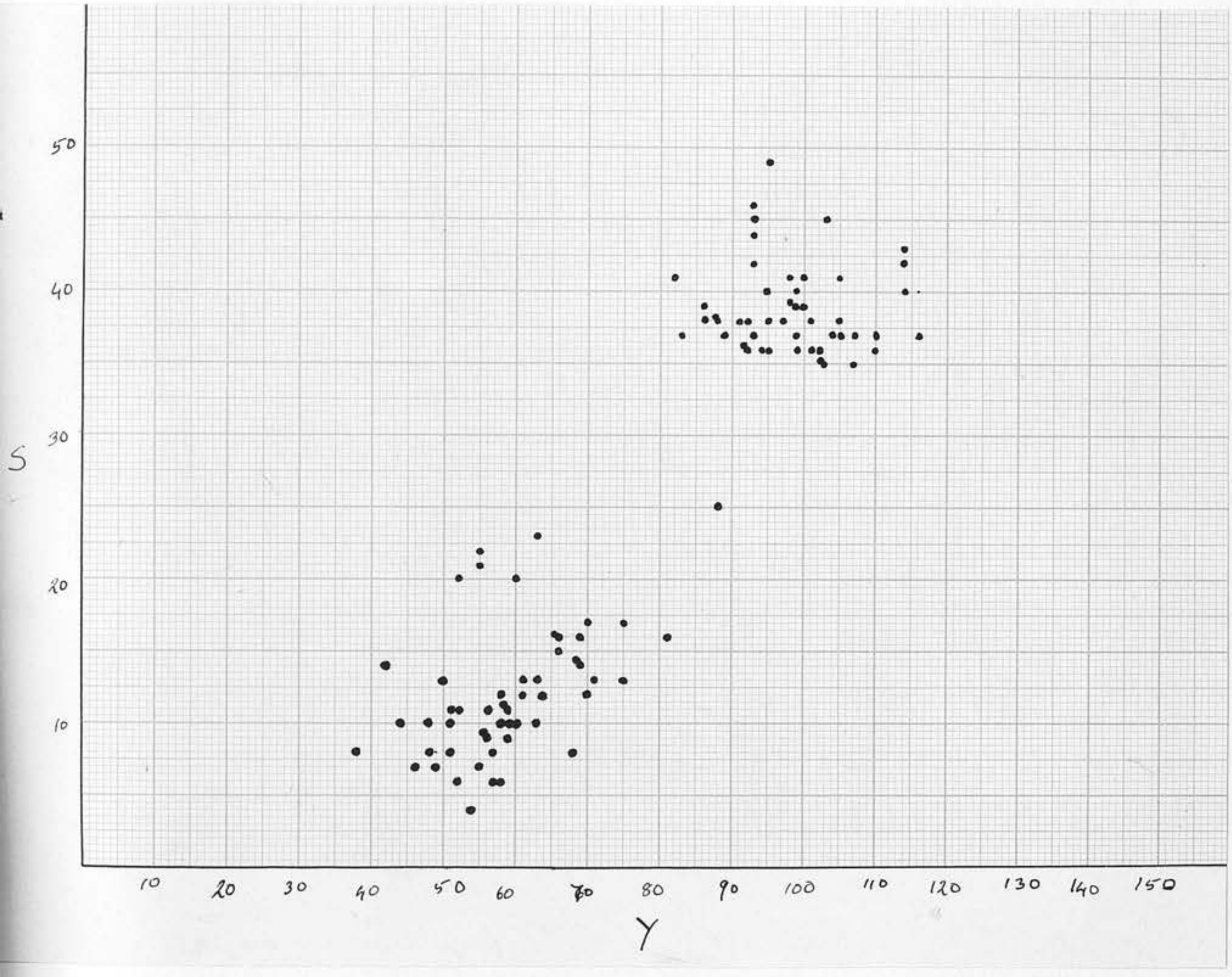


Fig. 51. Scatter diagram of S and Y for the plants from which the discriminant function was calculated.

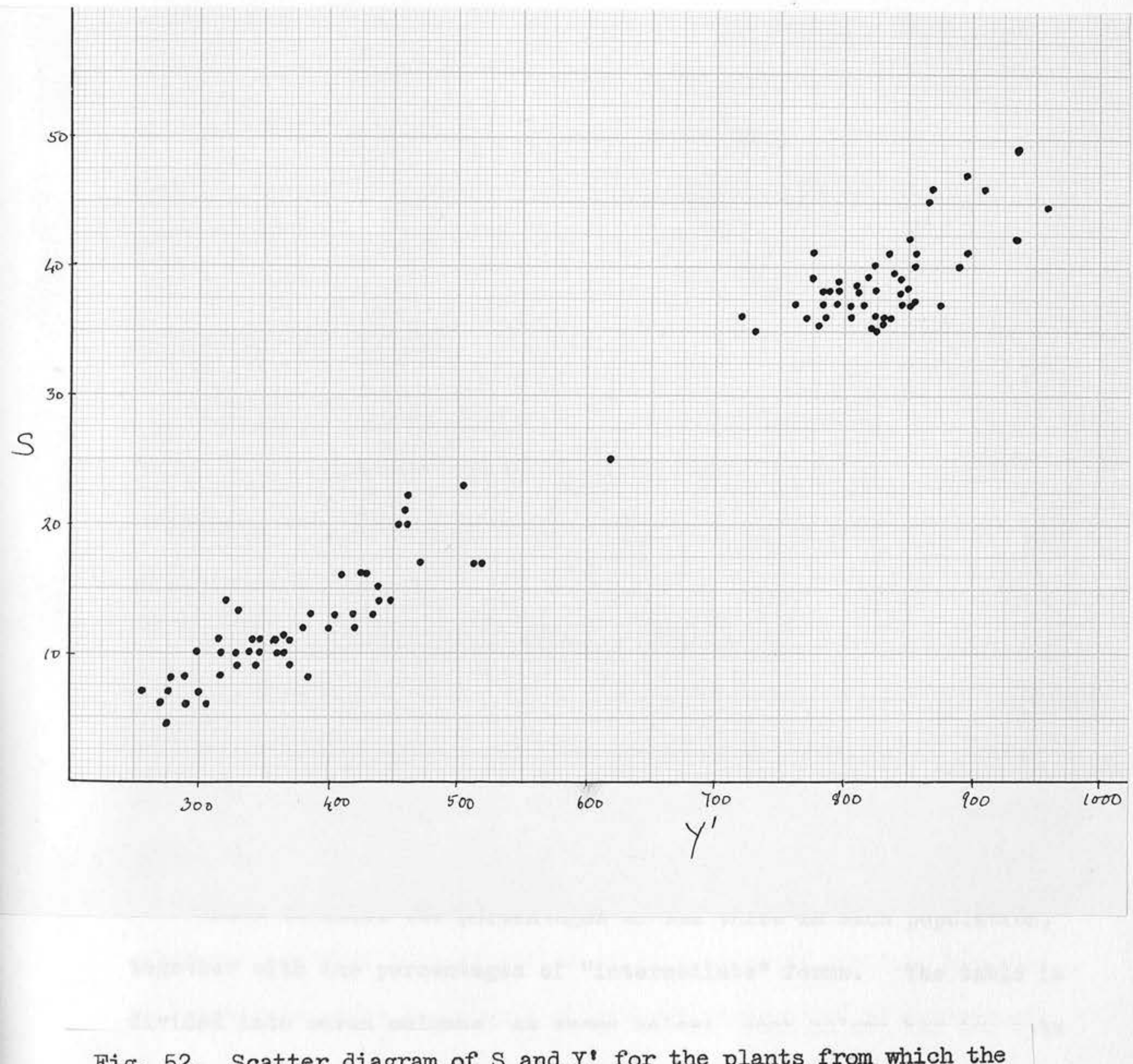


Fig. 52. Scatter diagram of S and Y' for the plants from which the discriminant function was calculated.

index alone, and it tends to obscure what is possibly the true relationship of the plants as shown by the simple index Y. The calculation and application of a discriminant function seems to be an unnecessary amount of extra work where multiflora and congesta are concerned, although it may be of great value in other groups of plants, where the index is made up of component characters bearing a different relationship to each other.

H. POPULATION ANALYSIS.

The fifty populations making up the mass gatherings have been considered collectively in the previous sections; a further study of some of them individually may illustrate the relationships of the plants in the field.

Appendix I contains a summary of the maxima, means and minima of each character, and of the three indices for every population, together with the standard deviation and variance where appropriate. Brief notes on the ecology, and on the structure of the population are also included.

Table 10 shows the percentages of the three in each population, together with the percentages of "intermediate" forms. The table is divided into seven columns, as shown below; each column has two sets of percentages. The ~~first~~ second set of percentages is based on the values of X and Y, and the divisions are as follows:-

X	Y	
less than 80	50 - 110	campestris
more than 90	more than 90	congesta
more than 90	less than 80	multiflora
80 - 90	more than 90	campestris/congesta
80 - 90	less than 80	campestris/multiflora
80 - 90	80 - 90	campestris/congesta/ multiflora
more than 90	80 - 90	multiflora/congesta

The ~~second~~ first percentage in each column is based on a modified interpretation of X and Y as indicated in section F. It was shown there that several of these "intermediates" are not really such, and that most plants with X between 80 and 90 are either multiflora or congesta. The only plants considered as being possibly intermediate between campestris and the other taxa are those where the index values of the seed length:width ratio and of the anther:stamen ratio are markedly divergent, i.e. the plant has a high value in one of these characters, and a low value in the other. The reduction in numbers of forms intermediate between multiflora and congesta is less marked when the modified interpretation of this index is applied, but the intermediate group contains a slightly different set of individuals. Some of these individuals have a value of Y greater than 90, but they also have a lax inflorescence; others have a value of Y between 80 and 90. The greater part of the group with Y 80 - 90 is assigned to either multiflora or to congesta.

TABLE 10

THE RELATIVE FREQUENCIES OF CAMPESTRIS, MULTIFLORA AND CONGESTA, AND OF THEIR INTERMEDIATES, IN EACH POPULATION

	camp. %		mult. %		con. %		camp./ mult.		camp./ con.	con./ mult.		camp./ con/ mult.	N
IA	83	83	14	11	3	3		3					27
B	8	9	75	57	17	17			4		13		24
C	3	3	49	26	42	42			3	6	26		31
IIA			69	69	25	25				6	6		16
B			26	13	68	74				6	13		31
C	83	83	10	3.5			7	3.5				10	29
D			41	41	52	59				7			29
IIF(i)					95	95				5	5		21
(ii)					100	100							26
(iii)a	23	21	8	7	69	69					3		30
(iii)b	56	56	8		36	36		4			4		25
(iv)	89	89	7				4	11					28
IIIA			89	89	8	11				3			36
C	8	8	89	83			3	6	3				36
B			100	97				3					37
D			26	18	69	66				5	16		38
IVA			28	17	69	69				3	14		29
B	3	3	27	23	70	67					7		30
C			13	3	76	73				11	21	3	37
VA	6	6	65	61	27	25				2	8		48
B			18	7	82	79			3.5		10.5		28
C			58	53	26	37				16	10		19
D			78	74	22	26							27
VI			83	83	17	14			3				29
VIIA			30	26	67	67				3	7		27
B	3	3	49	23	32	32			3	16	36	3	31

Table 10 (continued)

	camp. %		mult. %		con. %		camp./ mult.	camp./ con.	con./ mult.		camp./ con./ mult.	N
XIIA					85	71			15	29		7
B	100	100										11
XIIIA			40	35	60	60				5		20
B			36	27	55	55			9	18		11
C			5		85	95			10	5		19
XIVA	4	4	58	50	38	30		8		8		26
B			65	60	31	35			4	5		55
C			68	58	28	32			4	10		60
D			32	32	65	63		2.5		2.5		40
XV			18	18	75	82			7			28
XVI			69	46	31	31	3	3		17		35
XVII	7	7	32	18	61	50	11	7		7		28
XIX			54	46	38	15	8		8	31		13
XXA			38	37	54	53			8	10		39
B			100	94			6					16
C			17	11	83	78				11		18
XXI	100	100										27
XXII			66	66	34	28				6		32
XXIIIA			18	14	77	77			5	9		22
B			40	25	60	55		5		15		20
C	100	100										26
IIE	52	52	28	28	17	17			3	3		29
	pallescens											
XVIIIA	73	73	20	20	7	7						19
B	26	26	69	69	5	5						15

Figures 53 to 70 are the ogives of the X, Y and Z for each population. Those of X and Y show that in most mixed populations there are two groups of plants (i.e. there is a flat region, or a kink in the middle of the curve), with only an occasional intermediate plant. The only mixed population of congesta and multiflora, where mixed forms (Y = 80-90) predominate is in VII B.

Very few really pure populations of multiflora and congesta occur, although there are three gatherings of each which contain no plants of the other :- IIIB, IIIC and XX B, and II F (i), II F (ii) and XIII C respectively. Pure populations of campestris are found in II C, II F (iv), XII B, XXI and XXIII C.

Populations where campestris is mixed with multiflora and/or congesta include I A, B and C, II F (iii) a and b. In most of the populations other than those mentioned above there is a mixture, in varying proportions, of multiflora and congesta. It is these mixed populations which are the most interesting and which will be considered in detail in the following pages. The pure populations were used earlier to illustrate the types of variation within and between characters (sections D and E).

CAMPESTRIS mixed with MULTIFLORA and/or CONGESTA.

Two groups of populations were collected where campestris grew mixed with, or near, multiflora and/or congesta. These are I A, B and C, and the five gatherings which make up II F. They will be discussed in detail to illustrate the field relationships of campestris with the other taxa.

IA, IB and IC.

The locality where these were collected was near the village of Fortingal, in Perthshire. The plants were growing in a field which sloped at about 15 degrees to the east. It was drained by several small streams and ditches, and it had boggy patches in the lower part; the top of the field was relatively well drained, and much drier. Grazing was by sheep and cattle.

I A was collected in the dry part of the field, and is made up mainly of campestris; I B was from the damper part of the slope below I A, while I C came from the sides of a drainage channel running alongside A and B.

In the field it was apparent that I A consisted mainly of campestris, while I B and I C contained both multiflora and congesta. The proximity of the three taxa indicated that, if hybridisation could occur, this might be a favourable situation in which to find hybrids.

Vegetative characteristics are often most apparent in the field, and it was obvious that I A had much shorter stems that B or C. When the Z index is calculated, I A has a range of from 21 to 54, B of 36 to 80 and C of 46 to 105; the means were 39, 66.5 and 73 respectively, (fig. 53 a and b, 54 a). The analysis shows that a much greater difference exists between A and B than between B and C. The difference between B and C may be caused by the slightly higher proportion of congesta in the latter, but it is more likely that it is the result of the damper conditions in which I C grew. A scatter diagram of $\sqrt{L}$ and $\sqrt{H}$ for the three populations shows a slight discontinuity of variation in these characters, (fig. 78); the smaller group of plants consists mainly of I A, and the larger of B and C.

The ogives of X are also shown in figures 53 a and b and 54 b. In I A the mean is 74, with the mode between 70 and 75; most of the plants fall in a group around the mean, and are true _campestris_. Three of the plants, however, have a value of X between 96 and 100, and there is one with X = 112; these four plants are _multiflora_ or _congesta_. In I B and I C the mode lies between 101 and 105, and the means are 101 and 105 respectively. In B two plants are separated from the main group (21 plants), while in C there is one plant isolated from the remaining 29; in these gatherings the majority of the plants are _multiflora_ or _congesta_ (50 in all), and the remaining four are _campestris_. If a scatter diagram of X and Z is made (fig. 79) two quite separate groups of plants are seen, the group with the higher values of both X and Z corresponds to _multiflora_ and _congesta_, and is composed of I C and B with four plants from I A, while the group with the lower values is _campestris_, and contains most of I A with five plants from B and C.

The relationships of individual characters in populations I A, B and C are shown in the ogives in fig. 80. The stem height and leaf length show the same pattern, with A having the shortest stems and leaves, and C having the longest, while B comes between them, but nearer to C. In leaf width A has the narrowest and B the broadest leaves, C having a mean very slightly lower than B in this respect. This variation corresponds to the variation shown by the Z index, where B and C are close to each other, and A is considerably less.

Considering the characters which make up the X index, the lowest number of flowers and of heads in the inflorescence is in I A; B and C are about equal in these characters. The lowest mean size of stamens is in I C (index 32 = 1.6 mm.), I B is intermediate (index 30 = 1.5 mm.), and I A (index 26 = 1.4 mm.) has the highest mean, although single plants in B and C have larger stamens than any in A (the ogives are based on the index values, so this character, and the stamen ratio are reversed in their relationships). The anther : total stamen ratio shows a similar relationship, I A having the lowest mean of the index value (19, 0.62), I B is intermediate (33.5, 0.56) and I C has the highest (27, 0.51). The three plants with a value of 26 or more may be considered typical of <u>congesta</u> or <u>multiflora</u> in this character, while the remainder are typical of <u>campestris</u>. I B and I C approach more closely a normal distribution, but they both show a rather gradual increase at the beginning of the curve, which is not matched by a corresponding flattening at the top; this is presumably caused by the presence in each of one or two plants of <u>campestris</u>. In this graph I B is is again in a more or less intermediate position between A and C, although nearer to the latter. The seed length:width ratio might be expected to show a similar type of variation to the stamen ratio, and in fact it does. The difference between I A and B and C is much more marked than previously, and the two latter are more similar to each other. I A again becomes irregular in the upper part of the range, where the three multiflora or congesta plants occur; I B and I C are both slightly irregular at the lower end of the range, the former having three plants and the latter one, with exceptionally low values (campestris).

These cumulative curves, and the scatter diagram of seed and stamen ratios, show that there are no plants in these gatherings which may be said to be truly intermediate between campestris and the other taxa. The population I A contains mostly campestris, while B and C are mostly multiflora and congesta; in some of the characters, namely stamen size and anther:stamen ratio, and in the vegetative characters, I B occupies a position intermediate between I A and I C, although nearer the latter.

The Y index showed that I B was composed of about 75% multiflora, and 25% congesta, while I C had about 50% of each, with a much less distinct break in the distribution, and rather more intermediate values of Y. This distribution is paralled by the congestion index, but here it is more pronounced; 75% of I B have a value of S less than 25 (multiflora), while 17% have S over 30 (congesta), while the remaining 8% are between 25 and 27. The curve for I A is comparatively regular, flattening out slightly at the top, where a few plants of congesta are included. The curves for seed size

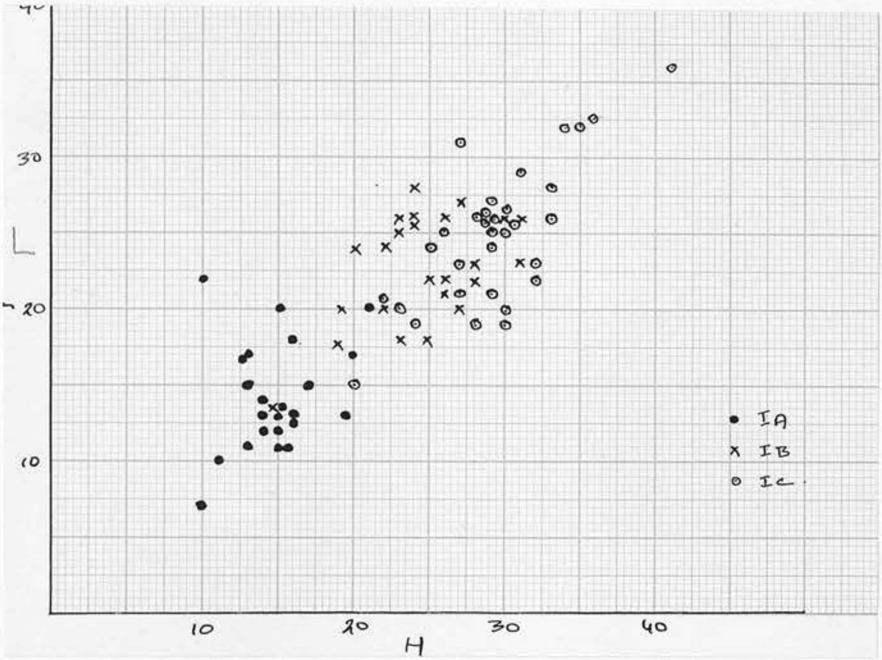


Fig. 78. Scatter diagram of L and H for populations I A, B and C.

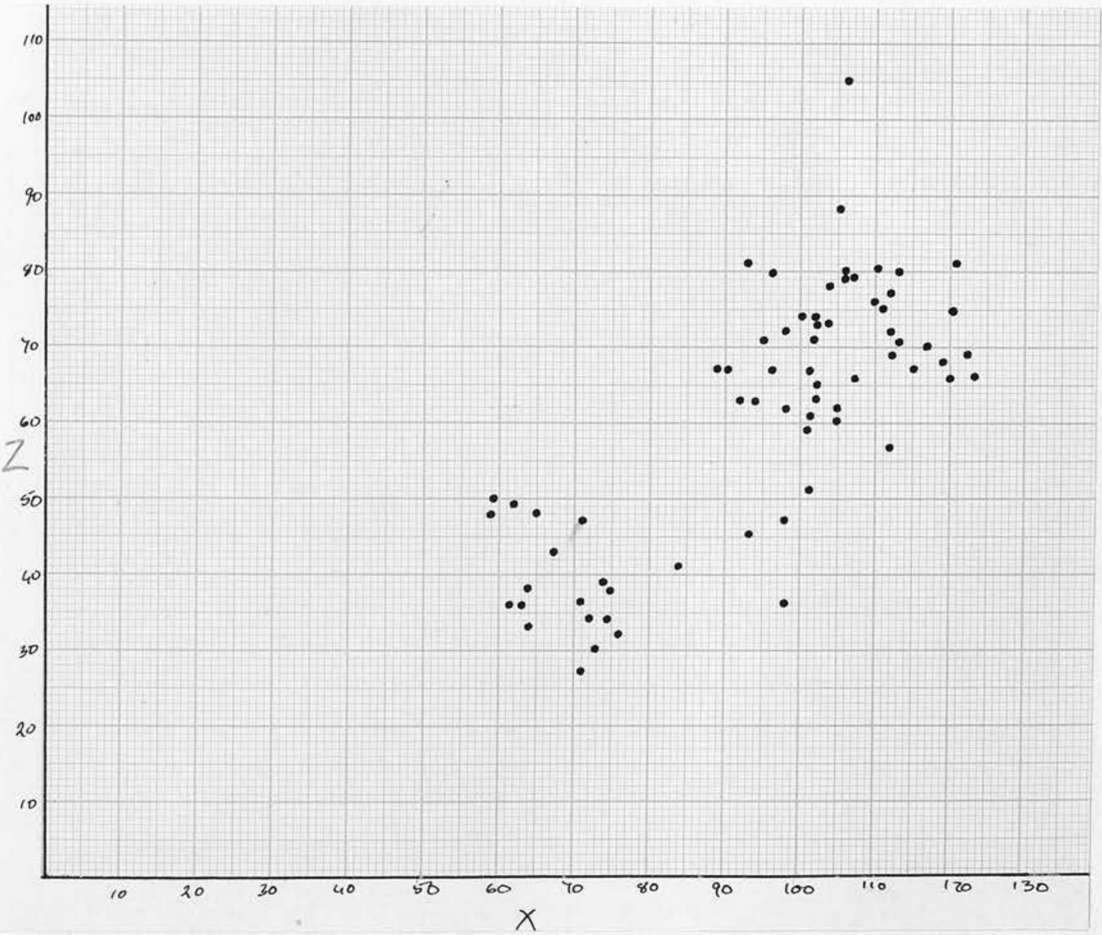


Fig. 79. Scatter diagram of X and Z for populations I A, B and C.

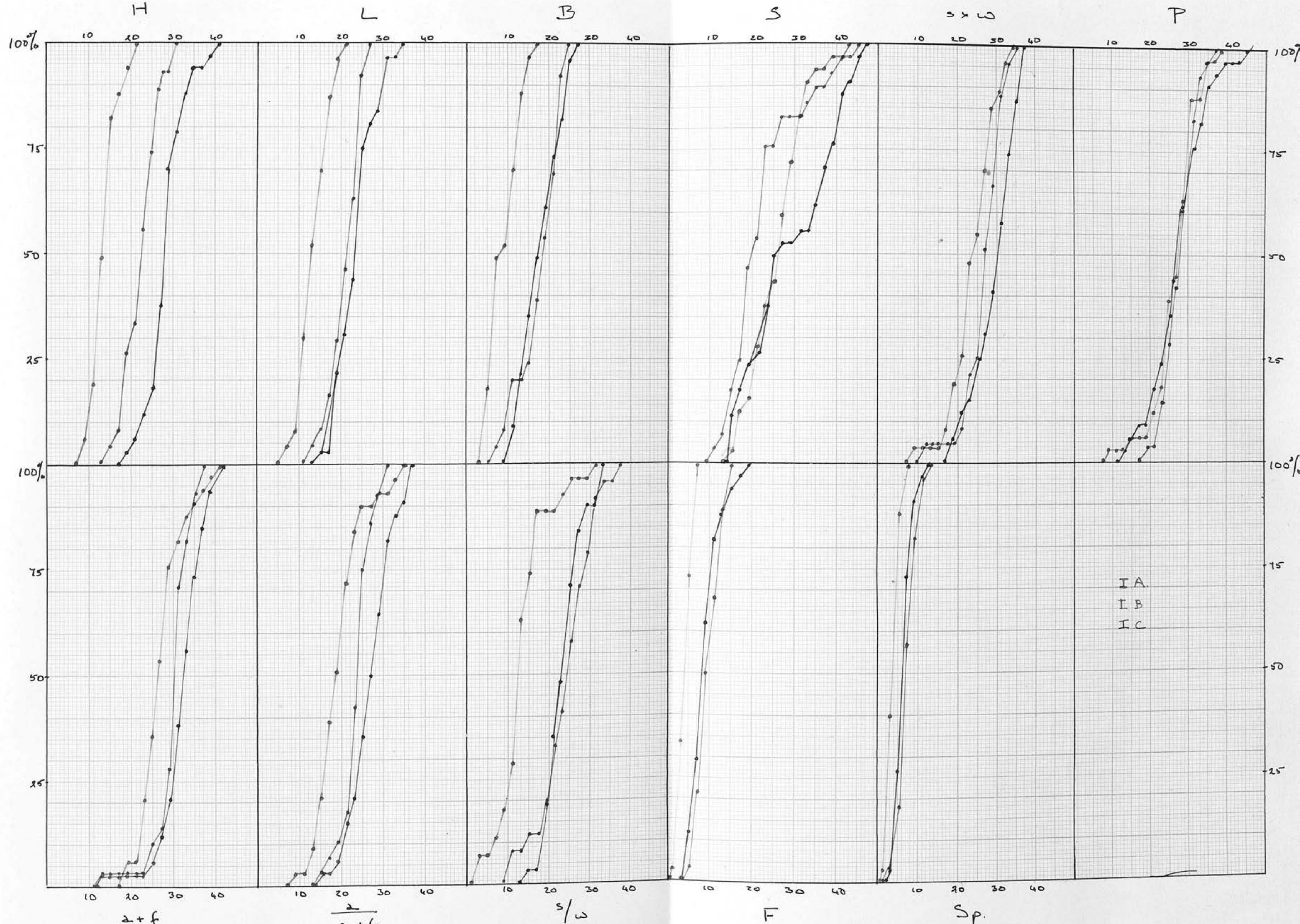


Fig. 80. Ogives of the diagnostic characters in I A, B and C.

show that I C has the largest seeds, I A the smallest, and I B is intermediate; the perianth size shows very little difference in the means, but I B has a smaller range than the other two. The differences in Y are therefore caused mostly by the differences in S, with the proportions in the different categories approximately the same.

These studies seem to indicate that, while the indices X and Y may be used to split the three populations among the three taxa, none is a pure population of any one taxon. There is some evidence, from the stamen characters, that I B might display a slight degree of introgression with I A, and it contains three plants of campestris, compared with ~~one~~ one in I C. This may be a reflection of two different factors:- (i) I A and I B had more common boundary that I A and I C, or (ii) campestris can hybridise less easily in the field with congesta than with multiflora, so that the population with the higher proportion of multiflora (I B) could contain more campestris genes than that with more congesta (I C). It seems that, in the absence of the necessary experimental evidence to back up the latter theory, the former is the more applicable to the present case.

II F

This community was situated in Glen Lyon, avout two miles north-west of I A, B and C. The glen here shows well developed glacial river terraces; the upper terraces support a grassland community, while on thelower ones there is a bog dominated by <u>Myrica gale</u>. This may be an effect of better drainage at higher levels. The ecological conditions of the area are described in chapter IV.

For the ecological descriptions the area was divided into four parallel zones: (i) the <u>Myrica</u> bog, (ii) the <u>Juncus</u> dominated strip at the edge of the bog, (iii) grassy slope and (iv) pasture. For the mass gatherings, (iii) was split into two parts, (iii)a and (iii)b, as it was wider than (ii) and was probably a transitional zone morphologically as well as ecologically.

The five gatherings, when first collected showed an obvious gradation in stem height, from tall plants in (i) to short plants in (iv). The ogives of Z in figure 54b to 56b show that this gradation is displayed by all the vegetative characters when combined into an index. A scatter diagram of $\sqrt{L} : \sqrt{H}$ shows that the gradation is continuous in these characters (fig. 81); (i) contains the tallest plants, and those with the longest leaves, and (iv) has the shortest stems and leaves. Each group merges into the ones below and above it, and there is no sign of a discontinuity.

Observation in the field showed that (i) and (ii) were more or less pure <u>congesta</u>, (iv) was pure <u>campestris</u>, and (iii) was a mixture of these with a few <u>multiflora</u> as well. A scatter diagram of two of the characters used to make the X index, the seed and stamen ratios, reveals a very different pattern from that of $\sqrt{L}$ and $\sqrt{H}$ (fig. 82). Instead of the plants showing continuous variation, and a strong positive correlation, there is a complete separation into two groups, and there is no correlation of the characters within the groups. The group with the lower values of seed and stamen ratios consists of all the plants in (iv), about 2/3 of (iii)b and about 1/3 of (iii)a, and corresponds to campestris. The second group has all of (i) and (ii), about 2/3 of (iii)a and about 1/3 of (iii)b, and corresponds to congesta. If introgression had occurred, it might be expected that the plants from (iii)a and (iii)b, although they are split into two groups, would occupy a position in those groups which was nearer to the other taxon than the pure populations, i.e. the range of variation of each taxon would be extended in the direction of the other. This is not the case, however, and the plants from both these gatherings are more or less randomly distributed throughout the groups.

Figure 83 is a "pictorialised scatter diagram" (Anderson, 1953), in which four other characters are superimposed on the scatter diagram of $\sqrt{L} : \sqrt{H}$, which is the same as in fig. 81, but the populations are not given different symbols. It is seen that the floral characters ($a + f$, $\frac{a}{a + f}$, s/w and F) are correlated with the vegetative ones, and show a gradation from small plants with low values of the floral characters, to large plants with high values for these characters.

These diagrams indicate that the vegetative characters are modified by the gradual change in the environment, so that there is a corresponding gradation of the Z index. Despite the vegetative gradation, the two most reliable floral characters, when used to make a scatter diagram, show no intermediate forms at all, and there is no evidence from them that introgression has taken place.

The ogives of X for these gatherings, (fig. 56b to 58b) also show that the plants are divided into two groups, and that there are very few plants which might be interpreted as being intermediate in the transitional gatherings of (iii)a and b. When all the values of X are combined in one histogram (fig. 84), there is a distinct gap between the two groups. The index shows that the plants of congesta in (iii)a and b have a rather lower mean and range of X than have (i) and (ii). This is possibly because the characters of number of flowers and of heads in the inflorescence are affected to some extent by the environment, so that fewer are produced when the habitat is less favourable, which results in a reduction of the value of X.

An examination of the ogives of the different characters for these populations (fig. 85) shows that in the vegetative characters there is a progressive increase in value of the mean, maximum and minimum from (iv) to (i) as would be expected.

The number of flowers and of heads in the inflorescence show a similar type of variation, but tend to come in two groups, one with

(i) and (ii), the other with (iii) and (iv); they are still arranged in the same order, with (i) the largest, and (iv) the smallest. The stamen size also shows the same pattern, (iv) having the lowest values, and (i) and (ii) the highest, with (iii)a and b between them. The seed and stamen ratios show a different pattern; in these the means show an increase in the same way as in the other characters, with (i), (ii) and (iii)a grouped together, and (iii)b and (iv). The three pure populations, (i), (ii) and (iv) all show the normal type of S-curve, but (iii)a and b show a bimodal distribution in both these characters, and reveal the mixed nature of these gatherings. In the stamen ratio the discontinuity in both populations is between 20 and 30; in (iii)a there is a sharp break $\frac{a}{a+f} = 22$ and 28, while in (iii)b there is a decrease in frequency between 20 and 24, but not a complete break. In the former population 21% of the plants fall in the campestris category, and in the latter 50%. The seed length:width also has normal distributions in (i), (ii) and (iv), and (iii)a and b again show discontinuities. In this case there are two small breaks in each population, both at values of s/w of about 20; about 23% of the plants in (iii)a are typical of campestris in this character, and in (iii)b 60%.

The ogives of the remaining characters, which make up the Y index, do not show very much. The congestion index shows that all the plants in (ii) are congested, but there is one plant in (i)

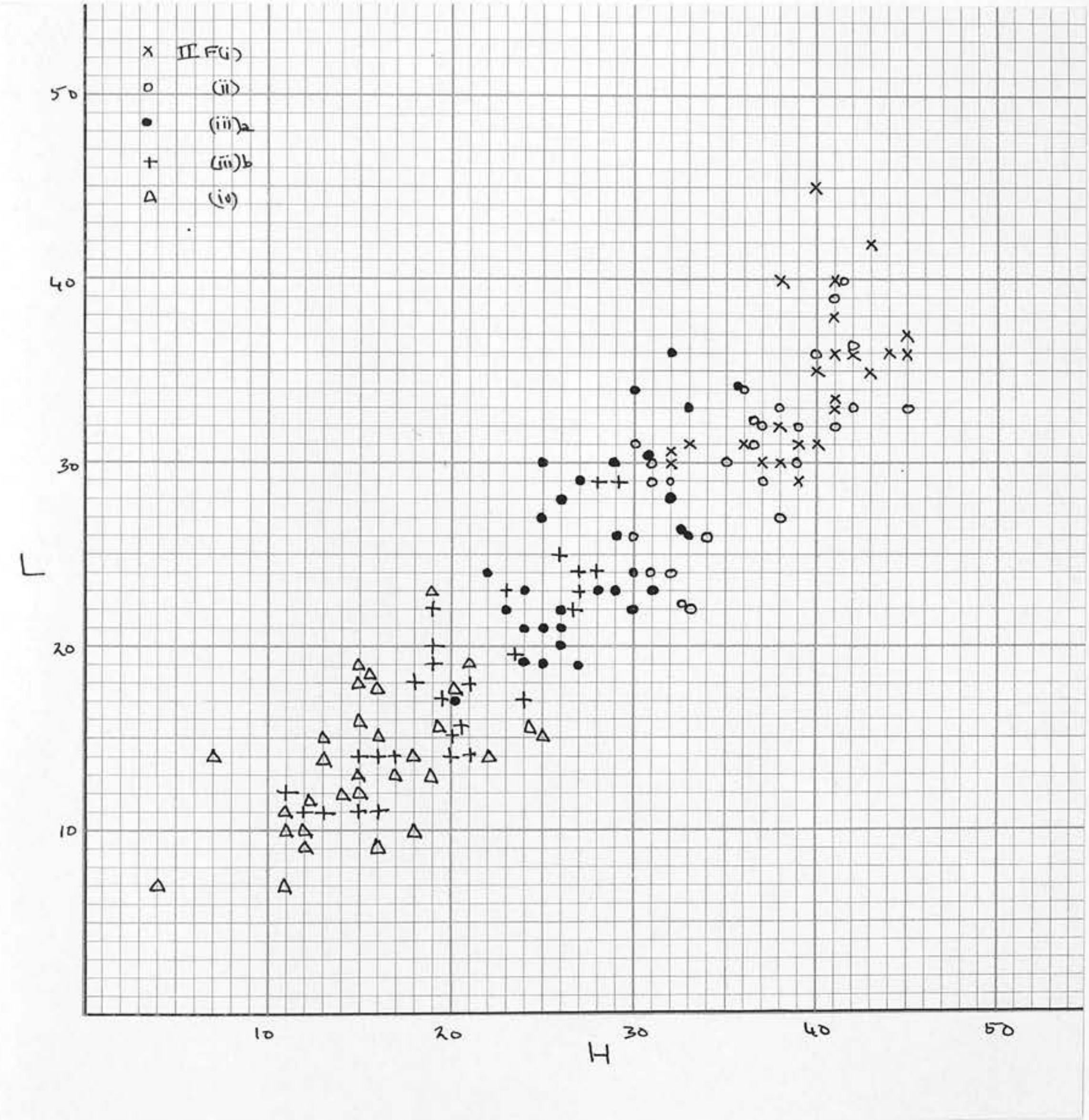


Fig. 81. Scatter diagram of L and H of populations II F (i) - (iv).

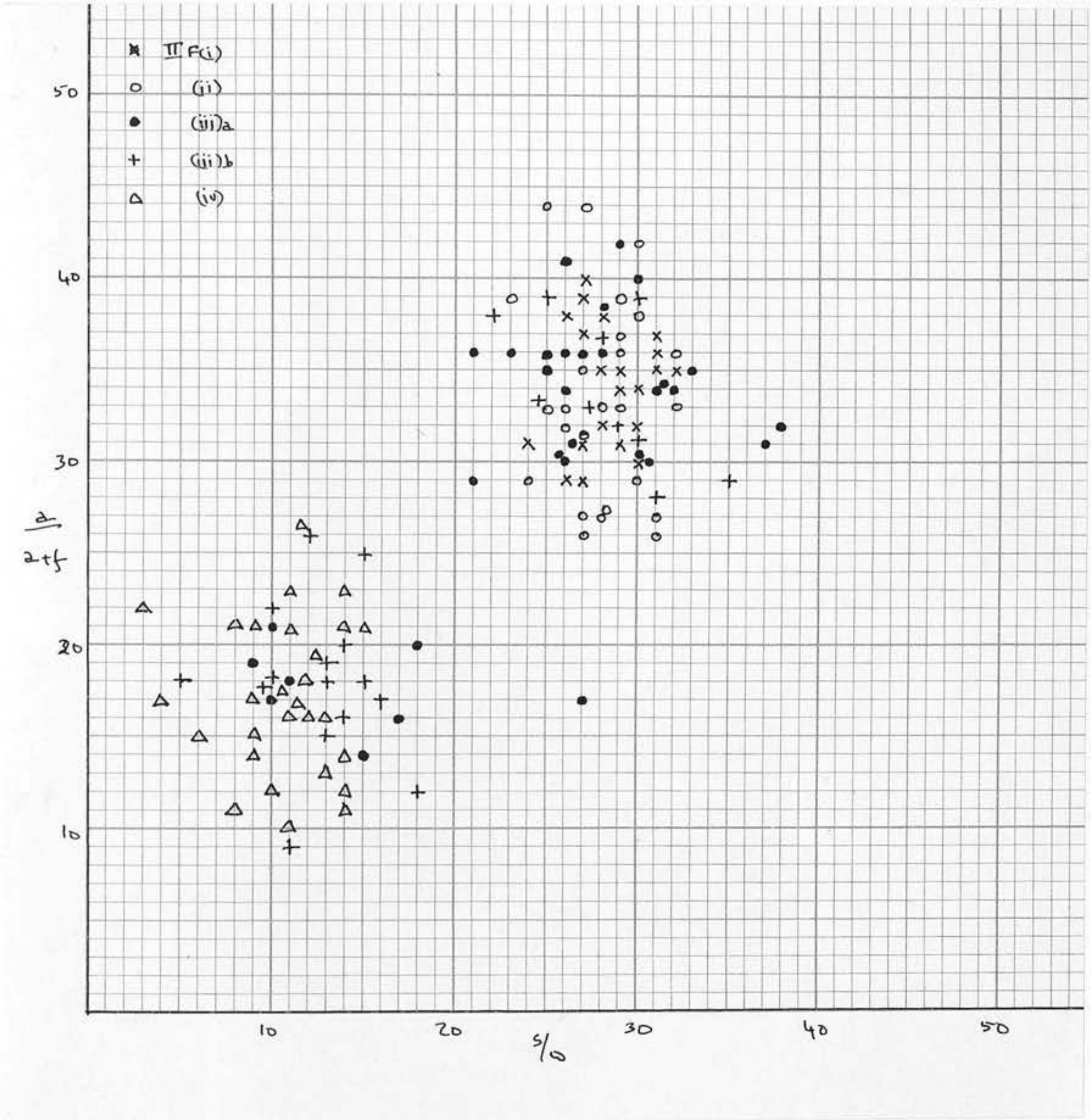


Fig. 82. Scatter diagram of $\frac{a}{a + f}$ and s/w for populations II F (i)-(iv).

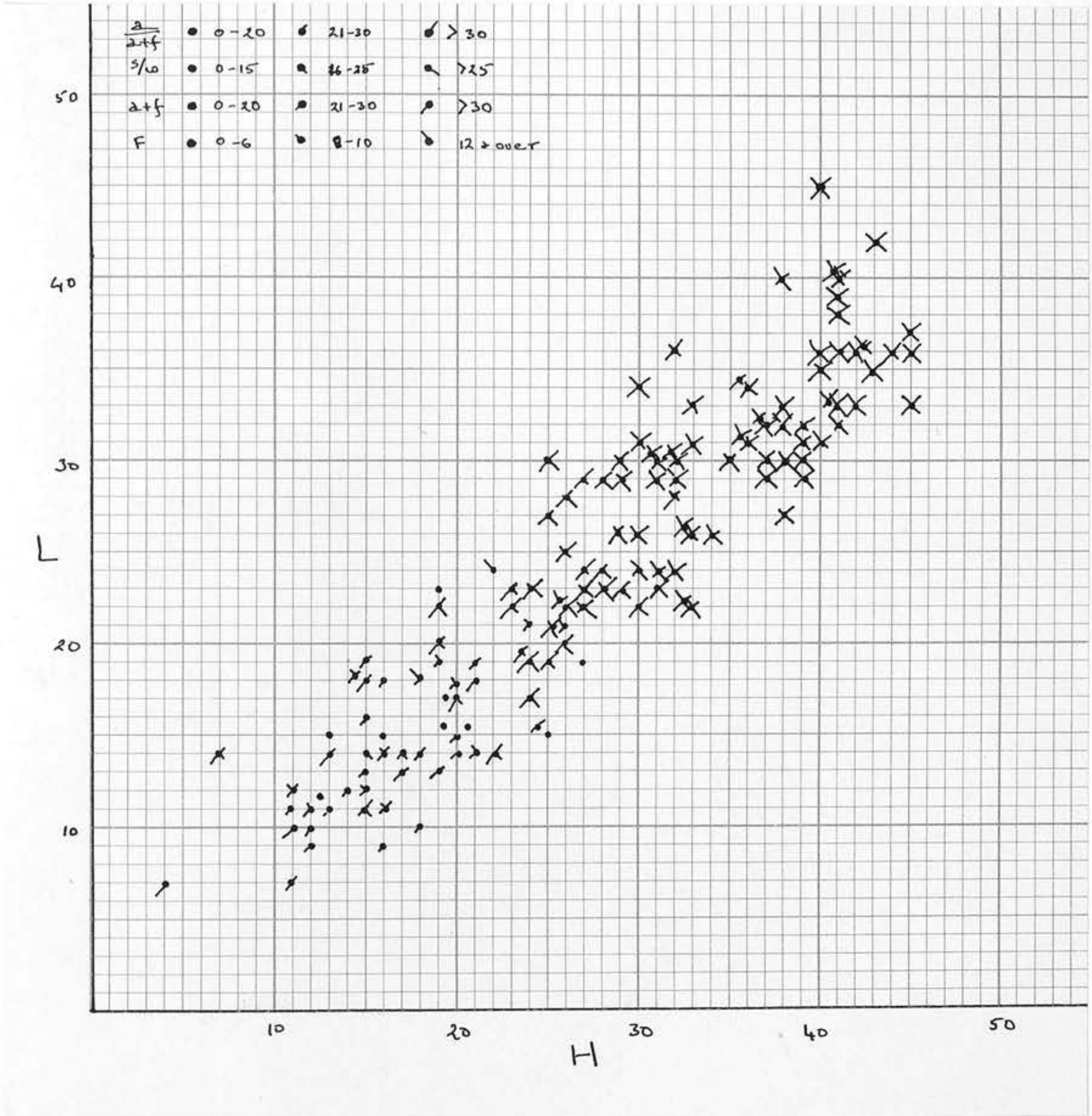


Fig. 83. Pictorialised scatter diagram of L and H for II F, with $\frac{a}{a + f}$, a + f, s/w and F superimposed.

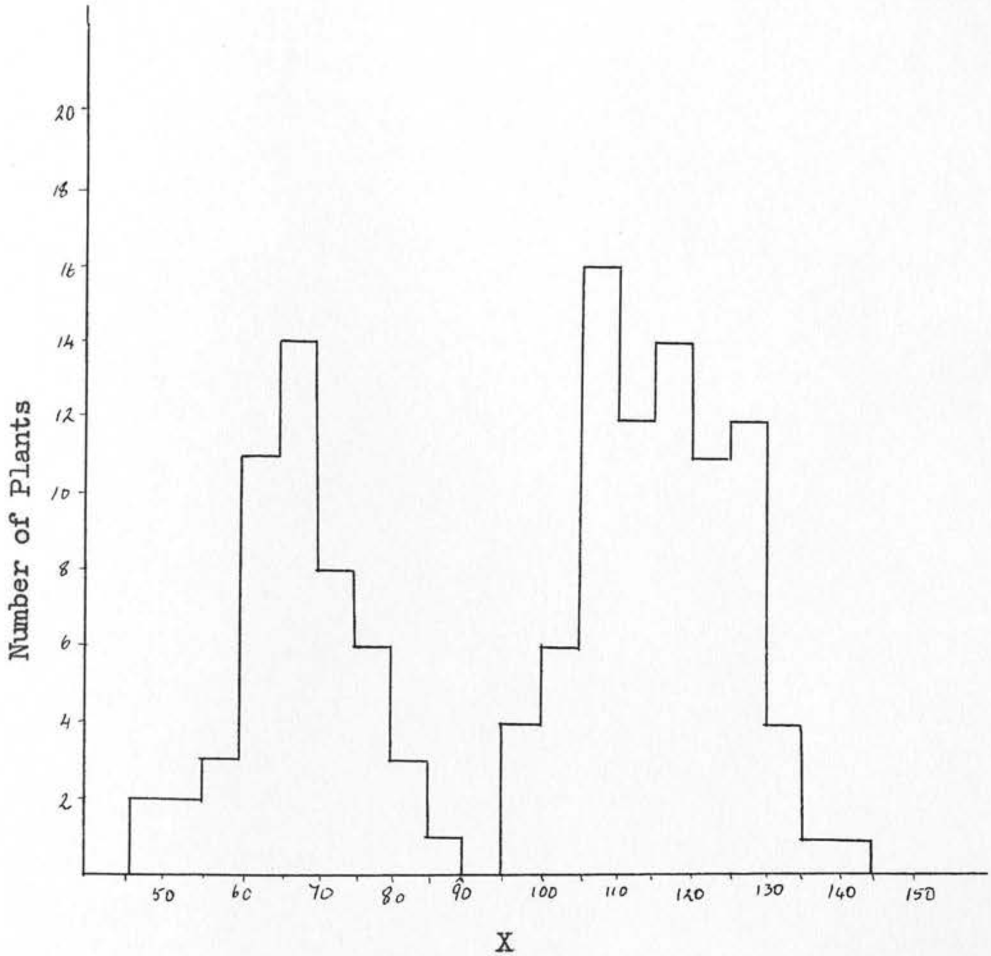


Fig. 84. Frequency histogram of the X index, for II F (i) - (iv).

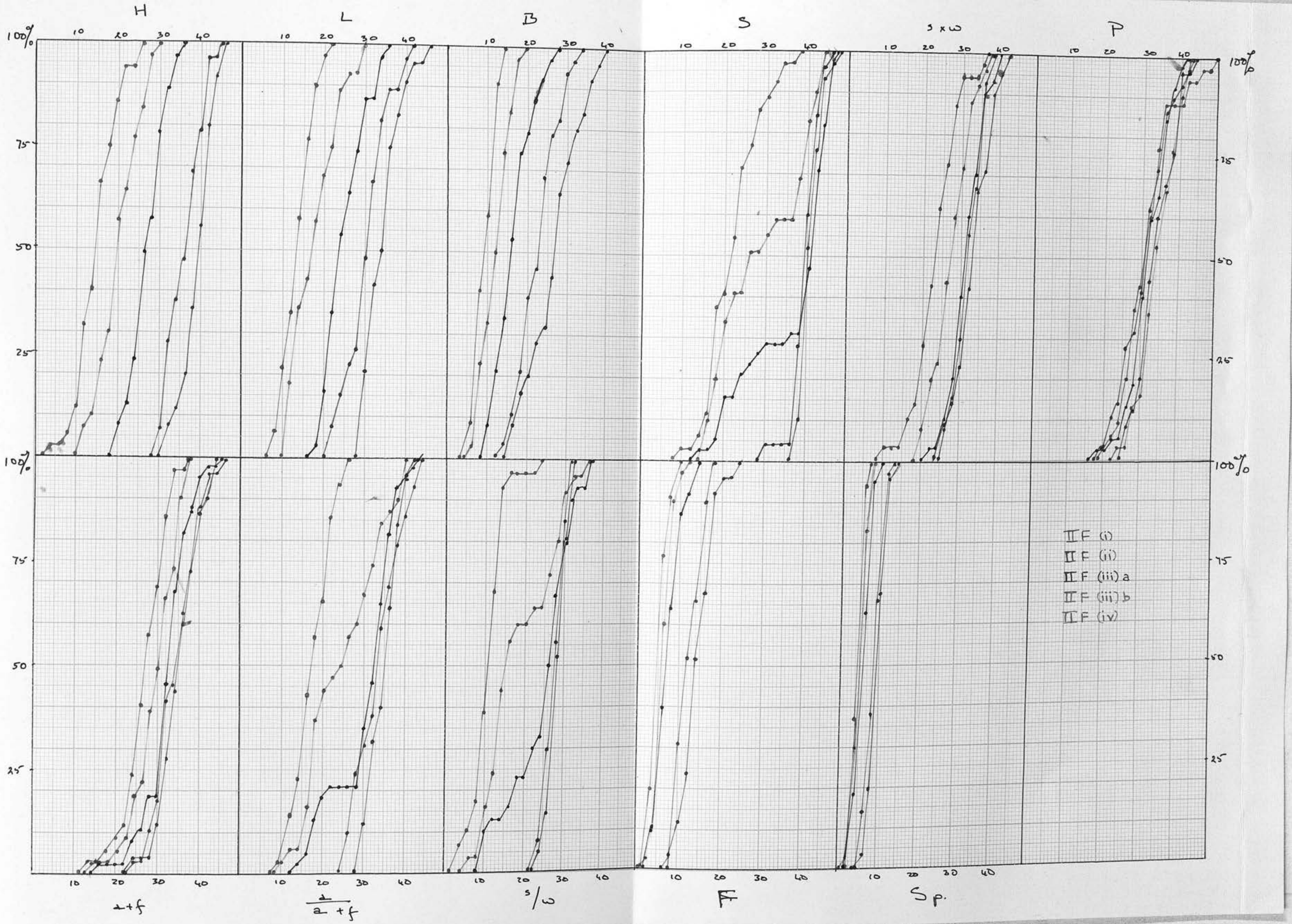


Fig. 85. Ogives of the diagnostic characters in II F.

which has a rather lax inflorescence. The other three populations show an increasing proportion of lax forms, as the proportion of campestris increases.

This group of populations shows no indication of hybridisation or introgression having taken place between campestris and congesta, or the few multiflora plants which were present. The first group of plants examined, I A, B and C also showed little sign of introgression, but there was a certain amount of evidence that I A (campestris) had rather more affinity with I B than it had with I C; the former contained a higher proportion of multiflora than the latter. In the case of the populations making up II F, there are only two plants of multiflora present, and the rest are all campestris or congesta. This might be interpreted as an indication that campestris might be able to cross occasionally with multiflora, in the field, but that hybrids with congesta would be very rare, if they existed at all.

MULTIFLORA mixed with CONGESTA.

Populations where multiflora and congesta grow mixed together may be divided into three groups:

a) Those in which multiflora and congesta occur in more or less equal proportions.

b) Those which are predominantly multiflora.

c) Those which are predominantly congesta.

As was stated earlier, absolutely pure populations of congesta and of <u>multiflora</u> seem to be relatively rare. Where a population contains over 80% of one taxon, with perhaps two or three plants of the other, these are usually widely separated from the main part of the population; this is illustrated by the ogives of Y for III A, VI, XV, etc. (figs. 59a, 64b, 70b, etc.) When there is a larger proportion of the minority taxon, a few intermediate forms frequently occur. There is only one population, VII B, in which intermediate forms predominate.

Table 10 shows the proportions of the different taxa in each population; the second figure in each column is based on the adjusted values of the indices, and these show a lower proportion of intermediate forms than do the first series which is based on the straightforward indices. The percentages of <u>multiflora</u> and <u>congesta</u> in the different populations are plotted against each other in figures 86 and 87, the former according to the indices, the latter according to the modified interpretation of them.

Both of course show a strong negative correlation; the groups of populations nearest to the axes are most nearly pure. The populations falling on the straight line drawn from <u>multiflora</u> 100% to <u>congesta</u> 100% are divided between these taxa; all the other populations contain either some intermediate plants, or some <u>campestris</u> (those containing all or much <u>campestris</u> were omitted), and the further away from the line, and nearer the origin they are, the greater the proportion of intermediate forms. In both graphs there is a slight gap apparent at about 50%, and no populations are an exactly equal mixture of the two taxa; this gap is more apparent in fig. 86 than it is in fig. 87, because in the latter some of the intermediate plants have been pushed into one or other of the taxa, and so have altered the relative proportions of these. Lines can be drawn, radiating from the origin, and passing through all points of equal ratio. The central line passes through 10:10, 20:20, 50:50, etc., the others are through 5:20, 10:40, etc. This gives the ratio of multiflora to congesta in the populations, irrespective of the number of intermediates present. A histogram can be made from each scatter diagram, to show the frequencies with which the populations occur between each pair of ratio lines; these histograms are inset beside the appropriate scatter diagrams. The histogram in fig. 86 shows a very distinct gap between + 1 and -1. with a sharp increase in the next category. Figure 87 shows a similar pattern, but there is a single plant between 0 and 1, and between 0 and -1; the other parts of the histograms are similar. In each case, the left-hand group of populations is predominantly multiflora, and the right-hand one congesta; in fig. 84 there are 17 populations in the multiflora group, and 22 in the congesta group. In fig. 85 there are still 17 in the multiflora group, and only 20 in congesta, so that the two between 1 and -1 must have come from the original congesta group. In both cases, there are 6 populations between -3 and the axis, which are the purest multiflora populations, and they are the same populations in each case; the same is true for the 9 populations between 3 and the axis, which are the purest congesta.

The populations can be divided into groups on the basis of these ratios, and arranged in increasing proportion of congesta and decreasing proportion of multiflora. The grouping according to fig. 86 is used.

1. between Y axis (-4) and -3.

III B	97 (100)% multiflora	III C	83 (89)% multiflora
XX B	94 (100)	VI	83 (83)
III A	89 (89)		

2. -3 to -2

V D	74 (78)% multiflora	V A	61 (65)% multiflora
II A	69 (69)	I B	57 (75)
XXII	66 (66)	XIX	46 (54)

3. -2 to -1

XIV B	60 (65)% multiflora	XIV A	50 (58)% multiflora
XIV C	58 (68)	XVI	46 (69)
V C	53 (58)		

4. +1 to +2

VII B	32 (32)% congesta	II D	59 (52)% congesta
I C	42 (42)	XIII A	60 (60)
XX A	37 (38)	XIV D	63 (65)

5. +2 to +3

XVII	50 (61) congesta	III D	66 (69)% congesta

XXIII B	55 (60)% congesta		IV B	67 (70)% congesta
XIII B	55 (55)		VII A	67 (67)

<u>6</u>. +3 to X axis (+4)

IV A	69 (69)% congesta		XX C	78 (83)% congesta
XII A	71 (85)		V B	79 (82)
IV C	73 (76)		XV	82 (75)
II B	74 (68)		XIII C	95 (85)
XXIII A	77 (77)		II F(i)	95 (95)
			II F(ii)	100 (100)

The two groups of more or less pure populations seem rather less interesting than the mixed ones, where the possibility of hybridisation or introgression would seem to be greater. Figure 88 shows the relative percentages of <u>multiflora</u> and <u>congesta</u> in the populations, which are marked individually on the diagram, instead of being represented by dots, as in fig. 86. The lines radiating from the origin divide the populations into groups according to the proportions of <u>congesta</u> and <u>multiflora</u> as in the tables above; the line drawn diagonally from 100% on the X-axis to 100% on the Y-axis passes through five populations which contain only <u>multiflora</u> and <u>congesta</u>, while the lines parallel to this indicate the proportion of each population which falls into neither of these categories. Most of the populations have less than 20% of the plants intermediate (a few of these may have one or two plants of <u>campestris</u>, which would be included with the intermediates here); eight populations have

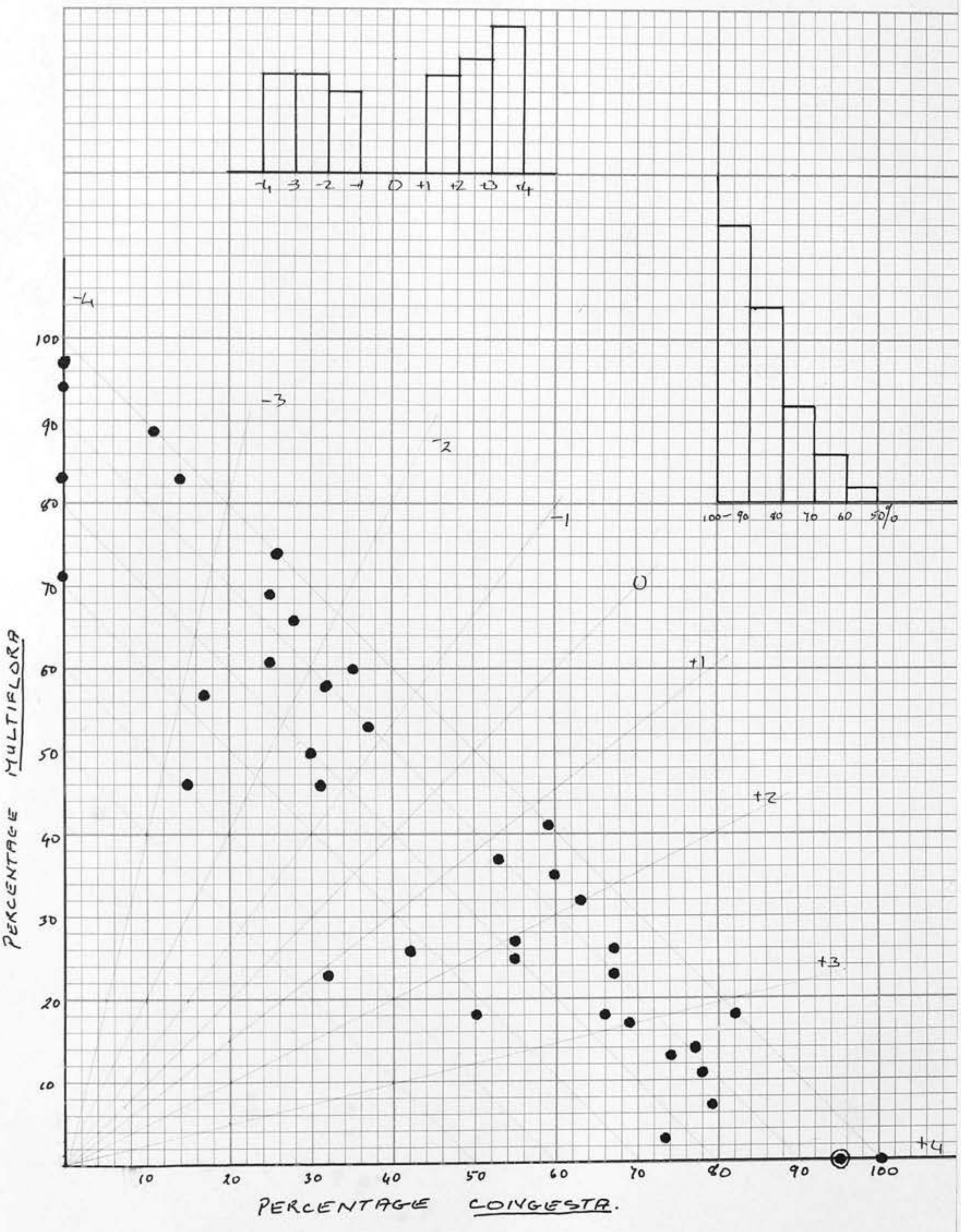


Fig. 86. Scatter diagram of the percentage multiflora and the percentage of congesta in each population, according to the Y index.

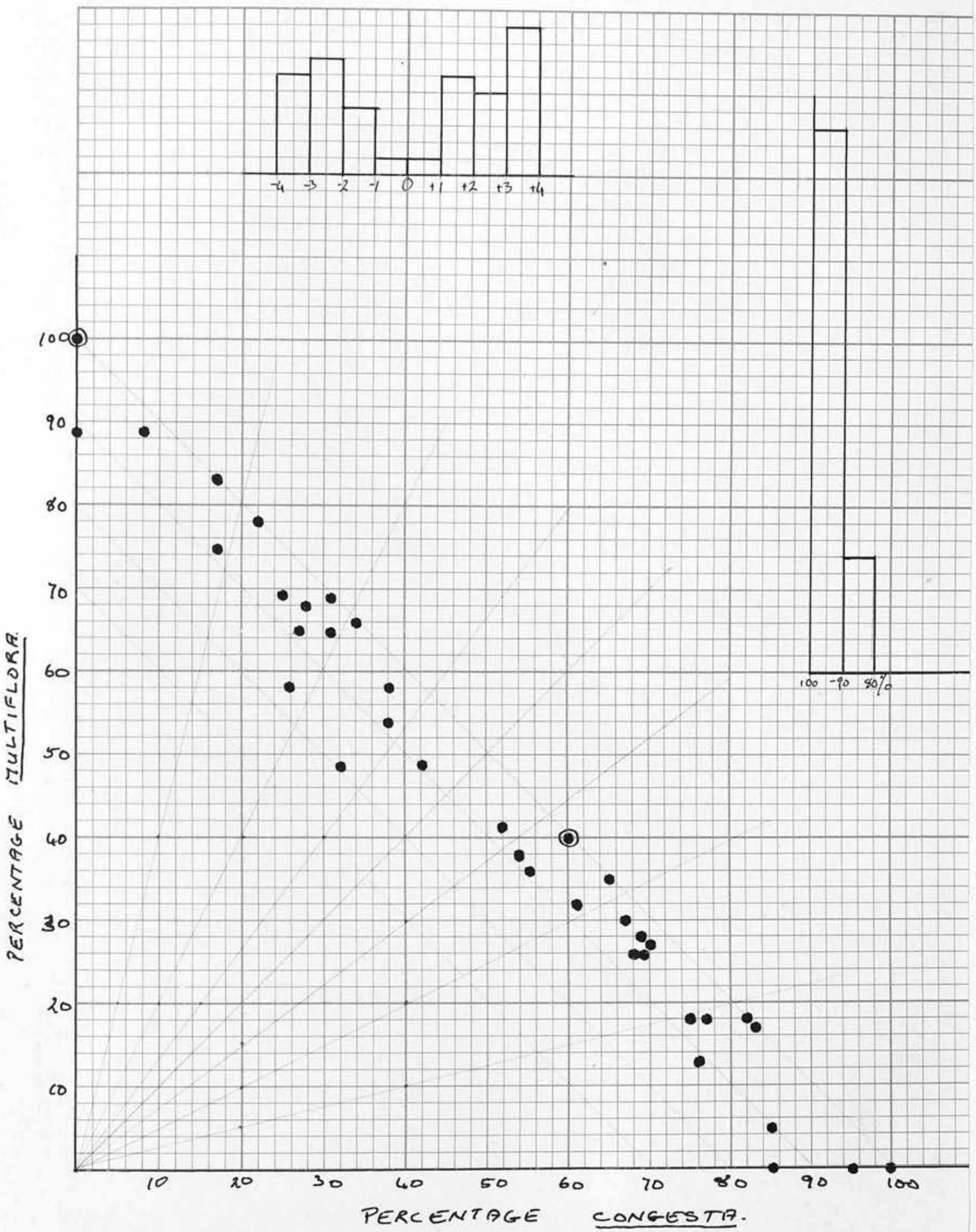


Fig. 87. Scatter diagram of the percentage multiflora and of congesta in each population according to the adjusted interpretation of the indices.

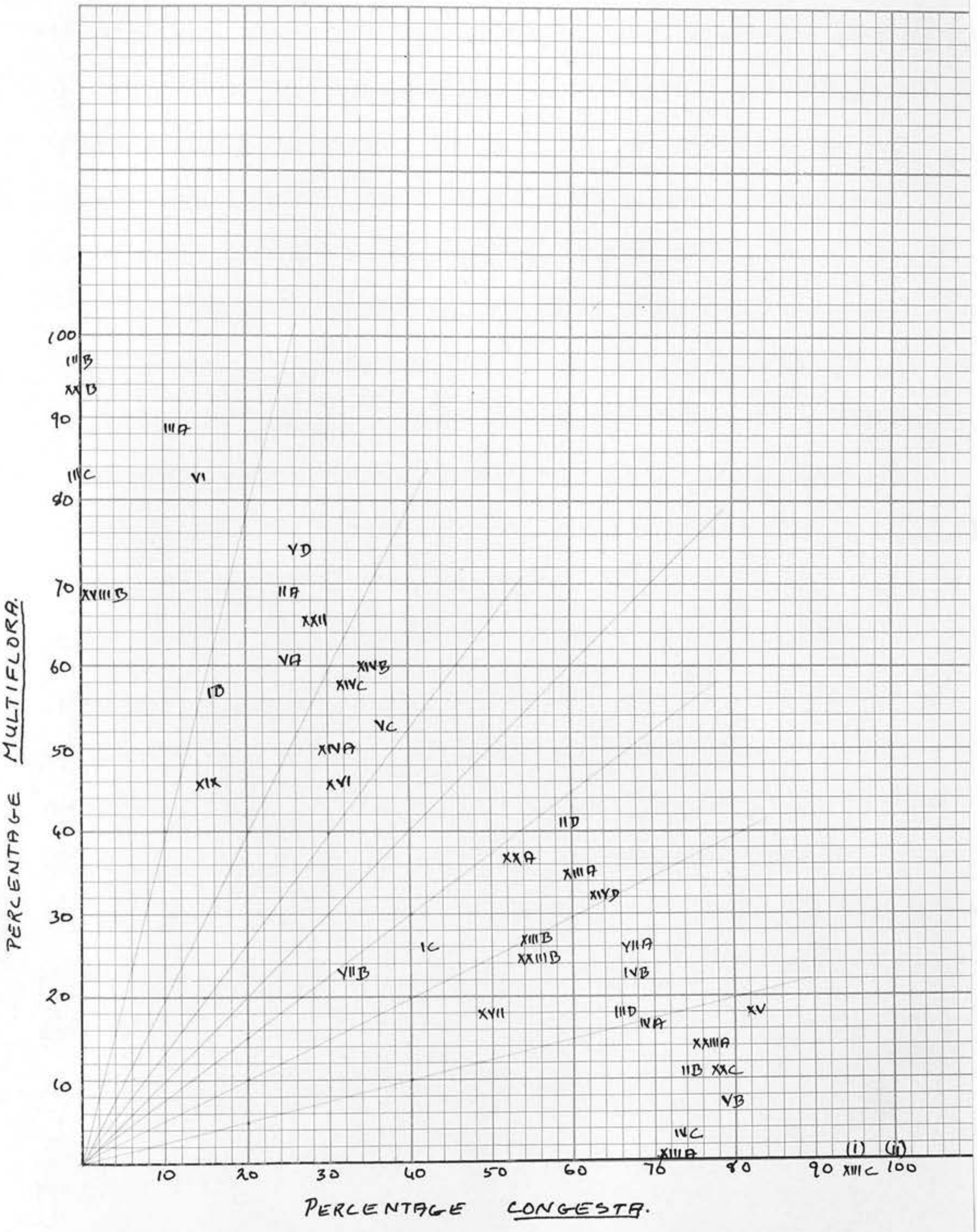


Fig. 88. Scatter diagram of percentage multiflora and percentage congesta, with population numbers.

between 20 and 40% intermediate forms, and one, VII B, has over 40%.

Not all the populations will be discussed in detail, but representative groups will be described to show the different relationships which are found in the field between these taxa. Summaries of the other populations are in appendix I.

The first group of populations, II A, B and D all have low proportions of intermediates; the first two are predominantly multiflora and congesta respectively, while the last is a mixture of the two, with no intermediates. The second group, III A, B, C and D show a similar pattern, the first three being largely multiflora and the last congesta. The third group, XIV A, B, C and D again have fewer than 20% intermediates, but they are all a mixture of multiflora and congesta, none having more than 65% of either taxon, and all falling within the lines +2 and -2 on the scatter diagram. The fourth group, I A and B both have over 20% intermediates, some of which may be campestris, and both are a mixture of the two taxa. The last group consists of the two populations VII A and B; the former is mostly congesta and does not have a very high percentage of intermediate forms, but the latter is a mixture of the two taxa and has an exceptionally high proportion of intermediate forms.

II A, B and D.

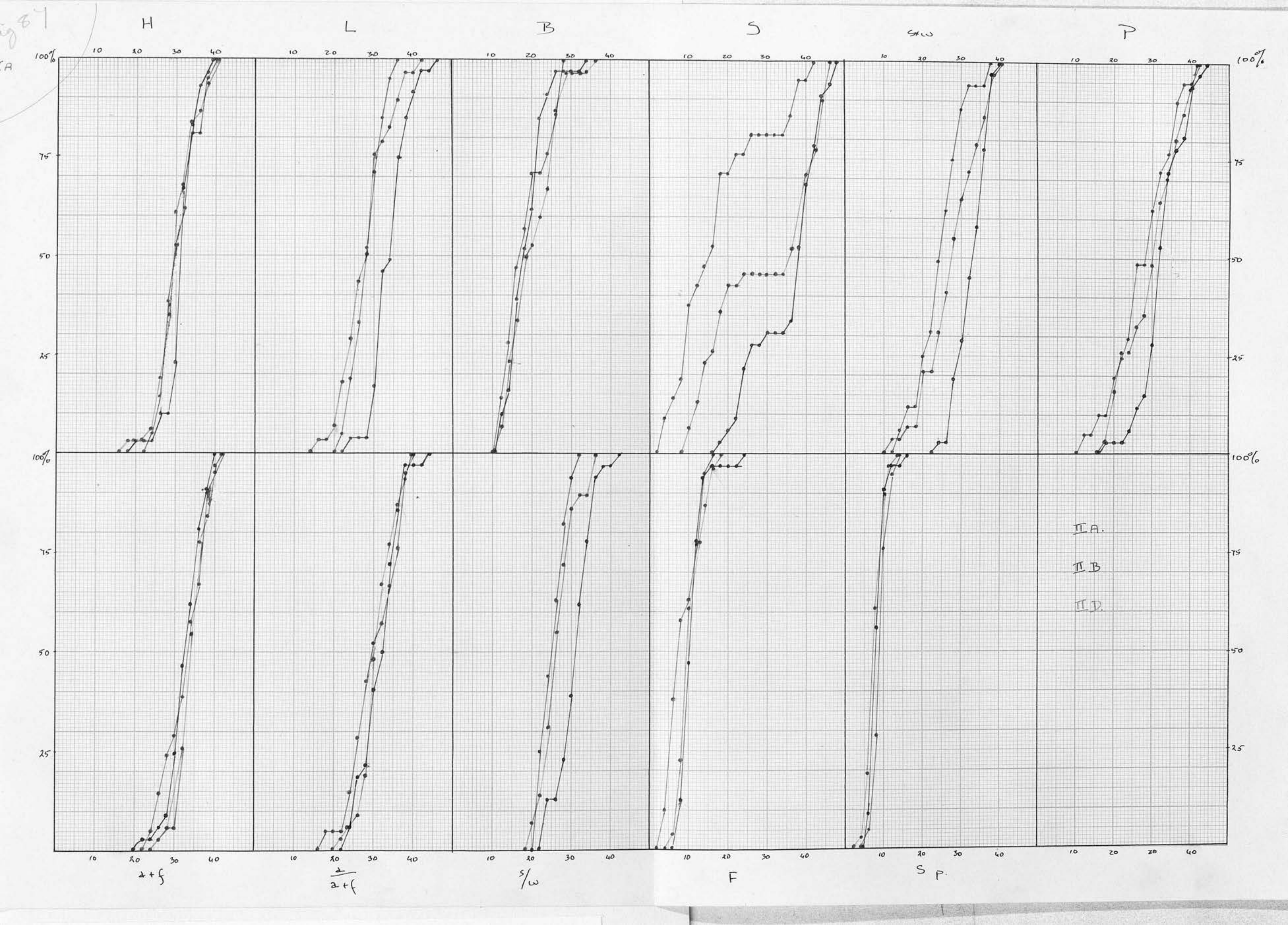
These populations were collected in Glen Lyon, in the same region as II F. II A is predominantly multiflora, II B congesta, while II D is a more or less equal mixture of the two.

Vegetatively, the populations are all very similar, as the ogives of Z in figures 54b, 55a and 56a show. The ogives of the individual characters making up this index (fig. 89) show that the variation in stem height and in leaf width is small, but that II B has a higher mean, maximum and minimum leaf length than the other gatherings; this results in a slightly higher mean value of Z for that population.

The ogives of X are correspondingly similar; I A and B each have only one individual with X less than 100, and II D has none. The means of X are 113, 116 and 112 respectively. The ogives of the individual characters in fig. 89 show that the populations are more or less the same in all characters making X, except for the seed length:width ratio, where II B has a rather higher mean than do the other populations.

The main differences between the populations lie in the characters making up the Y index. In the ogives of Y, II A shows two groups, one, containing 11 plants, with values of Y between 40 and 75, the other, with 5 plants having Y between 85 and 105. The break in the distribution in this population is between 75 and 85. In II B the curve is skewed, with the majority of plants in the upper part. There are again two groups of plants, the smaller group, about 35% of the population, has Y between 65 and 95, while the larger group extends from 100 to 125, and there is one plant between 95 and 100. In II D there is a more equal mixture of the taxa, with 42% multiflora and 58% congesta, and these have a very pronounced gap between them, from Y = 75 to 90. The point at which the two taxa diverge in the value of the Y index seems to depend upon which of the taxa predominates, and it tends to be lower when the population is mostly <u>multiflora</u>, and higher when it is <u>congesta</u>.

The ogives of the individual characters are shown in fig. 89; the most striking differences are in the congestion index, S. In II A less than 20% of the plants have a value of S higher than 26, and there is a distinct break between 26 and 34; the lower part of the curve is very steep from the minimum at 3 to 18, (71%), when it becomes irregular. In II B, less than 30% of the plants are below 26, when there is a slight step in the curve, and a most definite break between 30 and 35 - 69% of the plants have S greater than 35. In II D the break in the curve is between S = 24 and S = 44, with a small step at 20-22. The three populations each show a major break in the distribution of this character, at about the same place in each, although it varies in magnitude; the different positions of the breaks in the curves of Y most therefore depend on the two other characters which go to make it. The ogives for seed size show three more or less normal distributions, II A having the lowest mean, at 24, II B the highest at 33, and II D being intermediate at 27.5. The minimum of II D is nearer that of II A, while its maximum is nearer that of II B, so that the variance is greater than for the other populations. In perianth length the difference in the means is relatively less than it is for seed size, but the relationship of the populations is the same, with A the smallest, B the largest, and D falling between them. The two latter characters show no breaks in



H
L
B
S
S/W
P
10 20 30 40
100%
75
50
25
II A.
II B
II D.
α + f
α / α + f
S/W
F
S P.

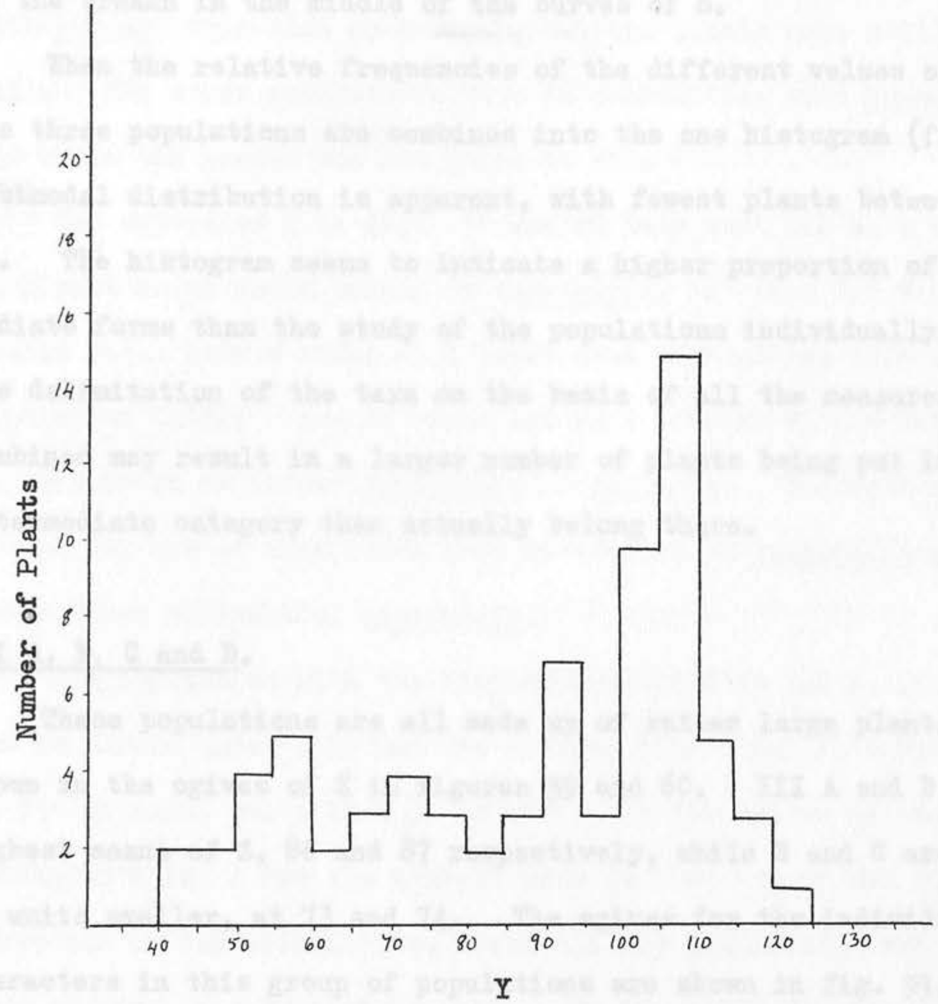


Fig. 90. Frequency histogram of the Y index for II A, B and D.

the curves, except at the ends where they show some irregularity, and in the middle of P for II A, but none of these is as distinct as the breaks in the middle of the curves of S.

When the relative frequencies of the different values of Y for the three populations are combines into the one histogram (fig. 90), a bimodal distribution is apparent, with fewest plants between 81 and 85. The histogram seems to indicate a higher proportion of intermediate forms than the study of the populations individually, so that the delimitation of the taxa on the basis of all the measurements combined may result in a larger number of plants being put into the intermediate category than actually belong there.

III A, B, C and D.

These populations are all made up of rather large plants, as is shown in the ogives of Z in figures 59 and 60. III A and D have the highest means of Z, 86 and 87 respectively, while B and C are about 10 units smaller, at 73 and 74. The ogives for the individual characters in this group of populations are shown in fig. 91. The stem height and leaf length show two pairs of populations, III A and D being the larger in each case, and B and C the smaller. The leaf length shows a similar pattern, but much less marked, and III D has a considerably higher maximum than any of the other gatherings. The differences in the Z index are therefore caused by the differences in stem height and in leaf length, which may have been influenced by the habitat and by the associated plants; III A was collected in a wood, and the Luzula was growing with very tall Juncus spp., which it more or less equalled in height. In III D the plants were again growing with Juncus, this time in a ditch, but the plants were still fairly tall. The other populations were in communities with Juncus spp., but where the ground was not quite so wet.

The ogives of X in figs. 59 and 60 show that III A, B and D have no plants which could belong to campestris, but that III C has seven plants which have a value of X lower than that of the main part of the population (20%); one of these has an X between 95 and 100, and must be considered as either multiflora or congesta. The rest are between 60 and 90, and of them, three must be counted as campestris and the other three as doubtful campestris.

The population with the highest mean of X is III A, in which there are no plants under 100, and the mean is 125; in III B and C the mean is 111 in each, while in D it is 110. In the ogives of the characters making up X III A has the highest mean in four out of the five. The exception is the stamen size, where all the populations are about the same in mean, and in distribution. In the anther:stamen ratio all the plants in A are over 25, B and D each have one plant under 20 and separate from the rest of the population, while C shows a gradual increas from 15 to 25, and a steeper curve above that value; the pattern for the seed length:width ratio is much the same, III A has no plants less than 20, D none less than 15, and B two under 10, isolated from the rest of the population. In these plants the seed and stamen characters are not correlated, so that the value of X is not brought down below 80.

In III C there is again a gradual increase, and here the two characters are correlated, so that there is a group of plants in the population which are nearer to campestris than to the other taxa.

The ogives of Y show a normal distribution in III B and C, with means of 64 and 67 respectively; in A the mean is 61, but there are a few plants, about 15%, which have high values of Y, and extend the range of the population to a maximum of 112; III D has a mean of Y = 96, and is mostly congesta with a few multifloras extending the lower part of the range. III B and C are therefore almost entirely multiflora (except for the campestris in C), A is multiflora with 11% congesta and one possibly intermediate plant, and D is congesta with about 25% multiflora. In A there is a sharp break between multiflora and congesta, but in D they grade into each other.

In the ogive of S the relationships of the taxa are much the same as in the Y index. III A has the lowest mean value, 12.5, but the upper end flattens out, and four plants have S greater than 25, two of these being truly congested, and over 35, and the others between 25 and 30. III B and C both show a normal distribution, and a very narrow range. III D has over 30% of the plants with S less than 30, but this part of the curve is very irregular; there are several "steps" in it, but the main disjunction seems to be between 30 and 32, and the upper part of the curve is quite normal. The remaining characters show a similar variation, but less pronounced. III A again has the lowest mean, in seed size, with a few plants at the top of the scale which are isolated from the rest, and which are the same as those with high values of S. In this population also the perianth size is the smallest, and again there is a "tail" at the top, where there is a small number of plants with large perianth segments. The three characters are correlated, so that the plants with high values of S also have high values of s x w and of P, and the index Y is correspondingly large, and separates them off from the rest of the population. In B and C the seed and perianth sizes follow the normal distribution, but in D the pattern is rather different. In D the mean is much higher than the other populations in seed size, and 11% of the plants have a lower value than the rest: these correspond with some of the 30% of lax forms in this population. In the perianth size there is no distinct break in the curve, but there is a slight flattening out in the curve between 30 and 35, and 45% of the way up, giving a slightly bimodal distribution; again, some of these are correlated with the lax inflorescences.

The incomplete correlation results in the gradation of multiflora into congesta in this population, while the correlation of the three characters in A serve to accentuate the separation of the congesta plants from multiflora. In A the break in the distribution is between Y = 65 and Y = 95, with one plant between these values, which is closer to multiflora and has Y less than 80, so might be included with that taxon. In D it is difficult to decide exactly where one taxon begins and the other ends, and it is possible that some of the plants are genuinely intermediate.

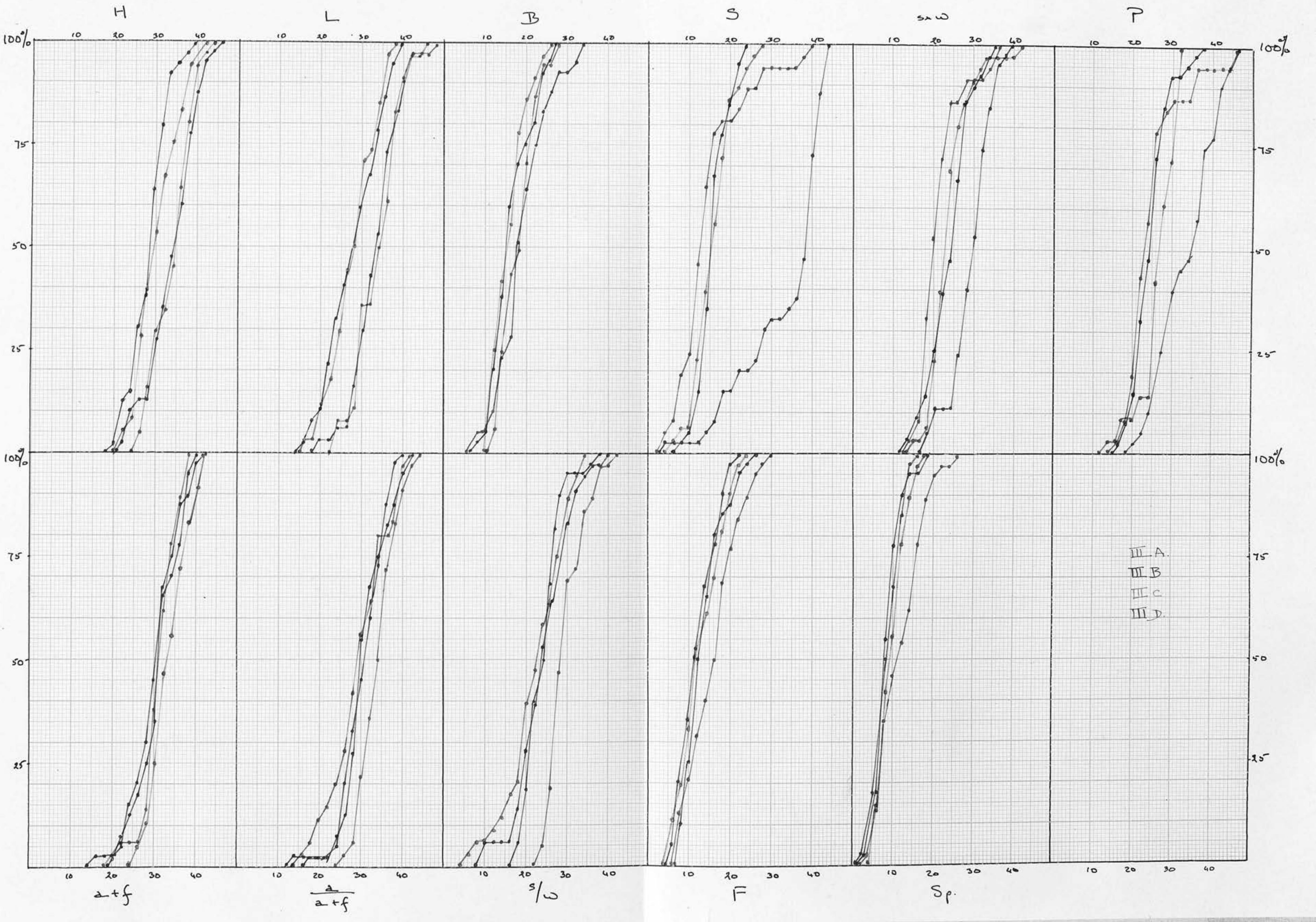


Fig. 91. Ogives of the diagnostic characters in III A, B^2, C and D.

III B and C have no congesta in them, but the latter has some campestris.

XIV A, B, C and D.

These populations were collected in a different area from the ones previously discussed, near Plockton, on Loch Carron in Wester Ross. They were gathered from an area which had once been mixed woodland, but had been felled several years before (B and C); from a damp area in a clearing in the part of the wood which remains, and along a path through the wood.

The ogives of Z in figures 69 and 70 show that XIV has the smallest plants, with a mean of Z = 71; B is very variable, has a mean of 83 and includes the highest values of Z in all the populations of the group. The means of C and D are 78 and 84 respectively, and both show relatively little variation. In fig. 92 the ogives of the individual characters are shown; the stem height and leaf length show some differences between the populations, but the leaf width is approximately the same for all four. In the stem height A is the smallest, and D the largest, with B and C approximately the same mean, although B has a greater range. In leaf length XIVAis again the smallest, but B has the highest mean in this character, and C and D are between them.

The ogives of X show that the only population with any plants with X less than 80 is XIV A, where there is one plant with X = 69; all the rest of the population are over 80. In the four populations there is therefore only one plant of campestris, so that the influence of this taxon on the populations much be negligible. The means of X for the populations show little difference, and are 107, 113, 112 and 115 for A, B, C and D respectively. All the characters making up the X index show very little variation between the gatherings; a single plant in A and in D have longer stamens than the rest, and there is one plant in A with a much lower seed length: width ratio, which is the plant of _campestris_ seen in the ogive of X for that population.

The ogives of Y for these populations present a rather different appearance from the preceding indices; they all have a bimodal distribution; A, C and D all have a distinct break in the curve at some point between Y = 80 and Y = 100, but B has a continuous distribution, although the curve is still bimodal. XIV A contains nearly 70% _multiflora_, and the break in the distribution is between X = 95 and 100; in XIV B there is a flattening of the curve between 75 and 100 to give 55% _multiflora_ and 25% _congesta_, but with no break between them; in XIV C 70% of the plants are _multiflora_, and the break is between 90 and 95; in XIV D only 35% of the plants are _multiflora_, and here the break is between 85 and 100.

The ogives of S show that C has 80% lax inflorescences, B has 70%, A, 60% and D 40%, which differ slightly from the percentages of _multiflora_ in the ogives of the Y index. There is a clear gap in the distribution of S at about the same place in each population, between 30 and 35. The ogives of the seed size show a similar pattern, but much less pronounced, with slight breaks at s x w = 30 in A, B and D, and a flattening of the curve in C. The means of A, B and C are all approximately the same in this character, but that of D is significantly larger. The curves of perianth size do not show any break, and A, B and C have again about the same mean, and D is again larger.

The ogives of these characters show that the differences in the distribution of Y are again caused primarily by the different proportions of S in each population. In general the other characters, seed and perianth size, are correlated with this character; if the correlation were perfect, the percentages of S and of Y in the populations would be the same, but they are only approximately equal, so that the correlation must not be perfect, especially in B, where the complete break in S is masked by the other characters to give a gradation in Y. Figure 93 is a scatter diagram of the seed size and the perianth size, with the congestion index superimposed. There is a reasonable correlation of the two characters, and most of the plants with high values of S (over 30) are found in the upper part of the range of the other characters, but there are several instances where the correlation is slight, and plants with high values of s x w or P have high values of S, or vice versa; these plants are possible intermediates.

Figure 94 is a histogram of Y for the four populations combined. There is again no distinct gap, and there appear to be more intermediate forms than when the gatherings were considered separately; the smallest number of plants is between Y = 86 and 95,

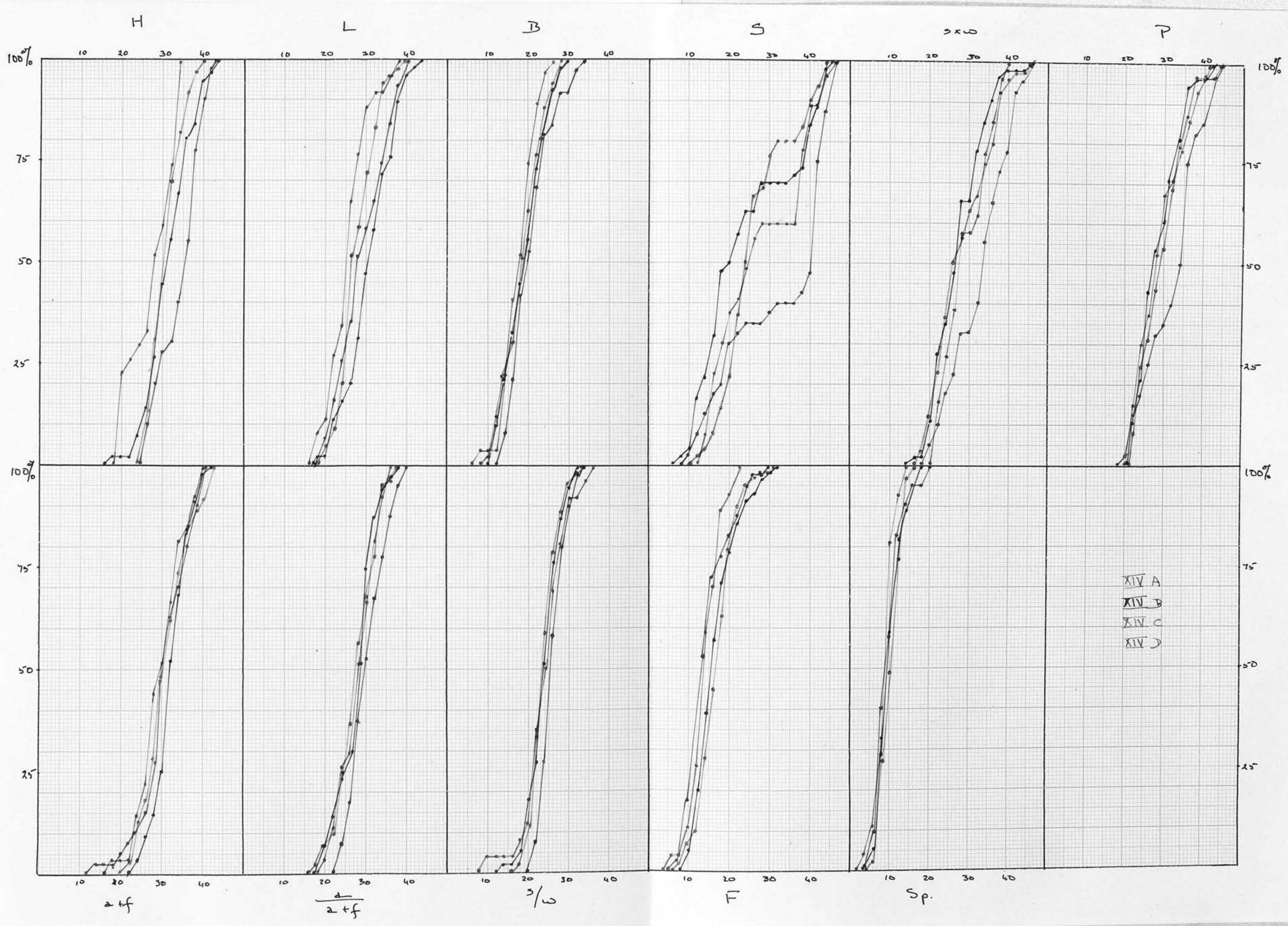


Fig. 33. Ogives of the dimensional characters in XIV A, B, C and D

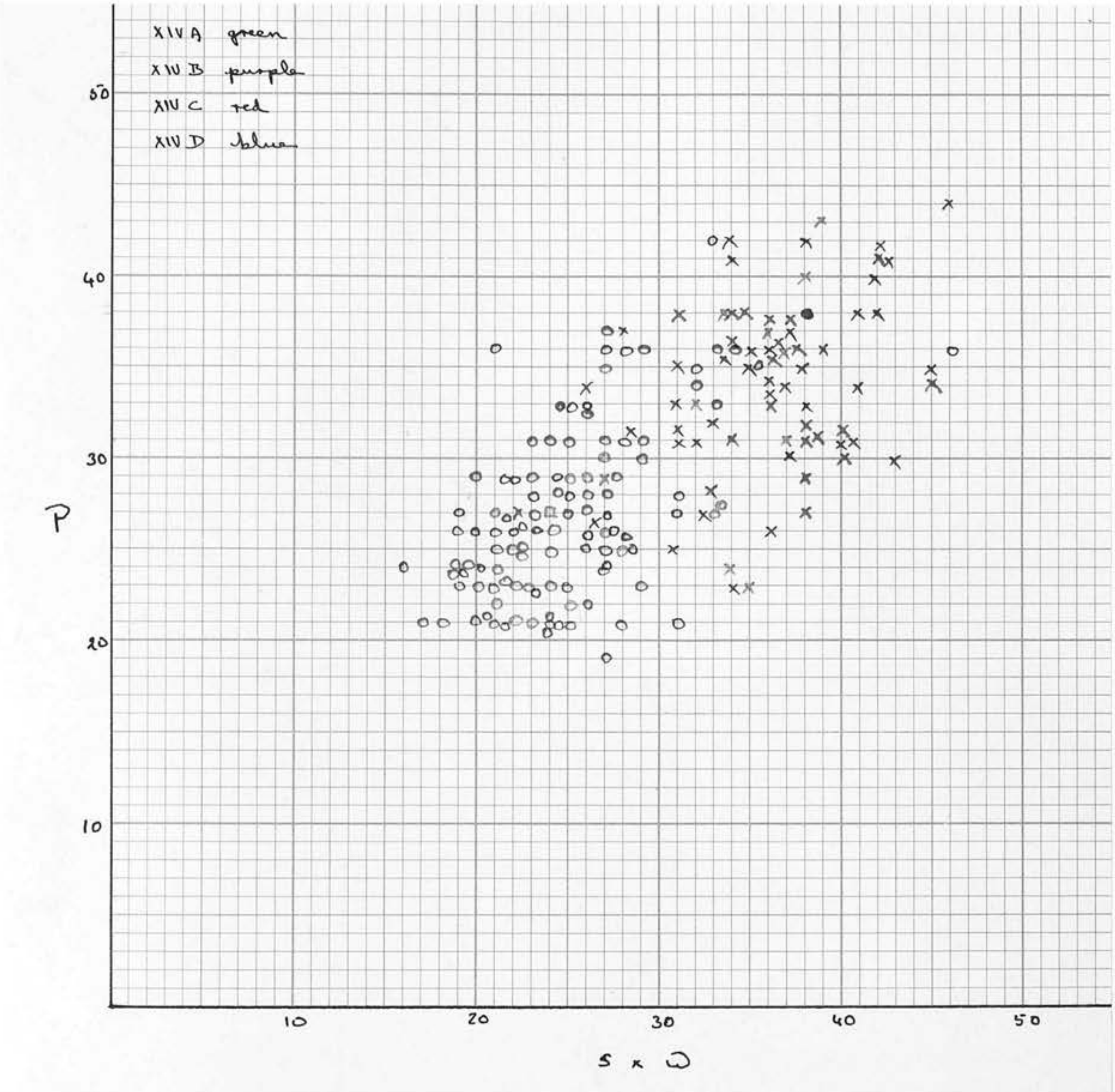


Fig. 93. Scatter diagram of s x w and P, with S superimposed, for XIV A, B, C and D. x = S greater than 30, o = S less than 30.

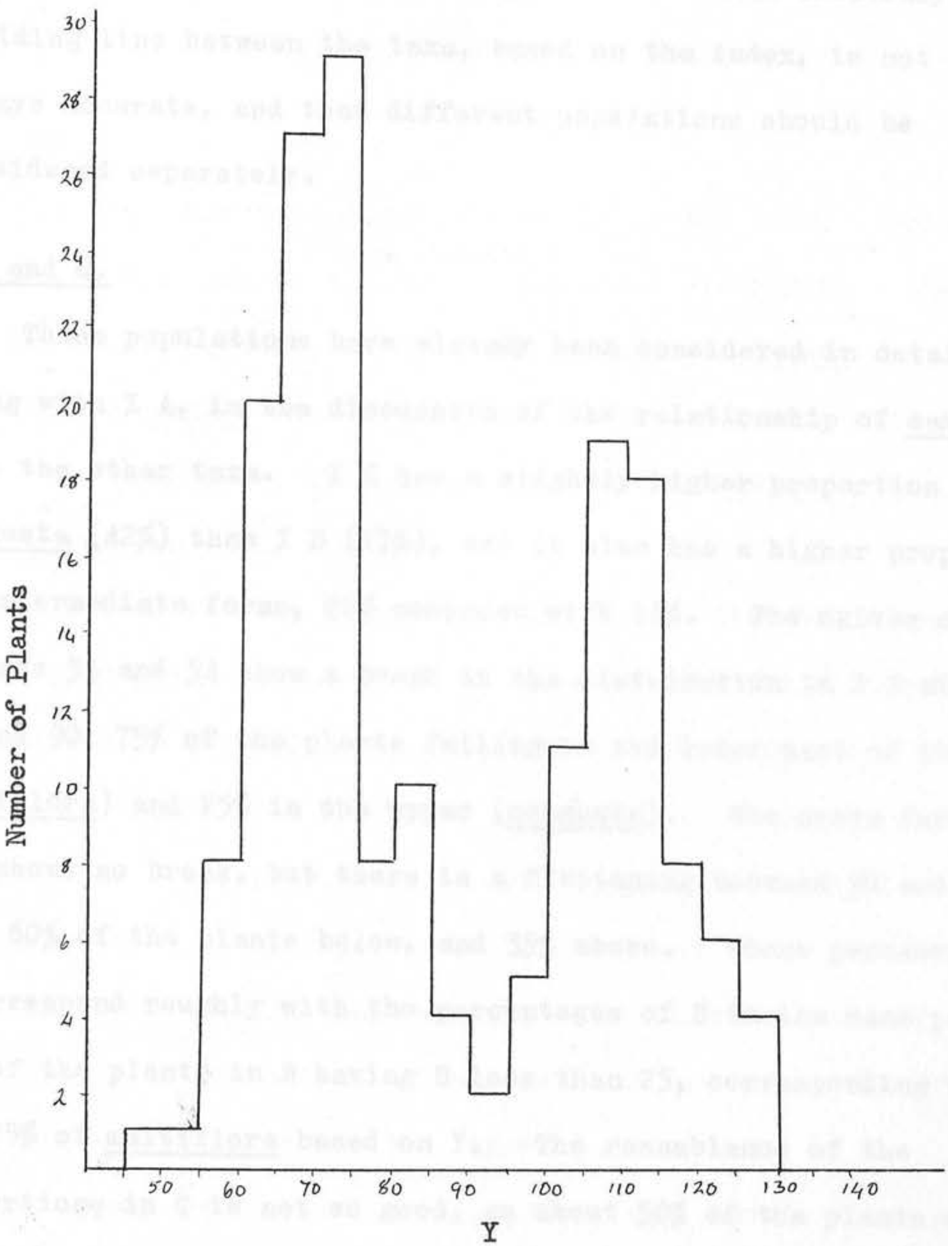


Fig. 94. Frequency histogram of the Y index, for XIV A, B, C and D.

with three plants in each of the two categories. These populations again show that perhaps the use of an arbitrary dividing line between the taxa, based on the index, is not always accurate, and that different populations should be considered separately.

I B and C.

These populations have already been considered in detail, along with I A, in the discussion of the relationship of campestris with the other taxa. I C has a slightly higher proportion of congesta (42%) than I B (17%), and it also has a higher proportion of intermediate forms, 26% compared with 13%. The ogives of Y in figures 53 and 54 show a break in the distribution in I B at between 85 and 90, 75% of the plants falling in the lower part of the range (multiflora) and 25% in the upper (congesta). The curve for Y in I C shows no break, but there is a flattening between 90 and 95, with 60% of the plants below, and 35% above. These percentages of Y correspond roughly with the percentages of S in the same populations, 75% of the plants in B having S less than 25, corresponding with the 75% of multiflora based on Y. The resemblance of the proportions in C is not so good, as about 50% of the plants are lax, and 50% congested, compared with 60% and 53% multiflora and congesta; the break in S is not so marked as it usually is, and the correlation with the other characters helps to increase the number of intermediates in this population.

In these populations again, the arbitrary division into multiflora, congesta and intermediates on the basis of the value of Y, and no consideration of the natural divisions of the population, tends to put too many plants into the last category.

VII A and B.

These two populations were collected on the lower slopes on Ben Lawers, near Lawers village. VII A was growing in a damp patch in rough grazing ground, and was associated with Juncus spp., Ranunculus flammula, etc. VII B was collected from a much drier part of the same area, and was associated with Festuca rubra, Anthoxanthum and other grasses.

The ogives of Z in figures 63a and b show that VII B has rather smaller plants than A, as might be expected from the differences in the habitats. The ogives of H in fig. 95 show that A has considerably higher values than B in this character, although they have the same minimum. The difference in leaf length is much less, but A is again the larger. In leaf width the means are about the same, but A has the higher maximum and minimum. If the difference in size is caused mainly by the habitat, then this has influenced the stem height far more than it has the other characters.

The ogives of X show that all plants in A have a value greater than 80, and there is only one plant in B which has X less than 80, so that all the plants in A are either multiflora or congesta, while there is one plant of campestris in B.

Examination of the individual characters making up X shows very little difference in any of them except for the seed length:width ratio, in which B has a lower minimum and mean than A, but the same maximum. The lowest values for the seed and stamen characters are all from the same plant, the one <u>campestris</u> in VII B. The difference in the seed character is probably caused by the fact that in B a large number of plants had only one seed in each capsule, instead of three; in these cases, the seed becomes rather more rounded than is usual in <u>congesta</u> or <u>multiflora</u>, and the ratio of length:width approached that of <u>campestris</u> (seeds from capsules with three seeds were used for the measurements if they occurred on the plant, but some had only single-seeded capsules, so they had to be used).

The ogives of Y show that VII A has two groups in it, 25% of the plants having a value of Y less than 80, and 75% more than 80, with a gap between 75 and 80. The ogive for B, on the other hand, does not show a bimodal curve, and the largest number of plants occurs between Y = 80 and Y = 90, the "intermediate" zone in most of the populations. In all the other populations where <u>multiflora</u> and <u>congesta</u> are mixed there is a bimodal distribution, with a minimum number of plants occurring somewhere between 80 and 100, and in no other population is the mode between 80 and 90. The presence of a significant proportion of <u>campestris</u> in the population might have helped to account for this distribution, but there is only one plant of <u>campestris</u> present. It would appear that some of these plants must be genuinely intermediate between <u>multiflora</u> and <u>congesta</u>.

Of the characters making up the Y index, S shows the greatest difference between the two populations; there is little difference in seed size, and the ogive for the perianth size is very irregular for both, but the maximum, mean and minimum is about the same in each. The curves of S show a bimodal distribution of this character in each population; VII A has 30% lax inflorescences and 70% congested, while B has 70% lax and 30% congested. Each curve shows a break, in A it is between S = 25 and S = 32, while in B it is between 30 and 38. The percentages of lax and congested inflorescences in A correspond more or less to the percentages of <u>multiflora</u> and <u>congesta</u> in that population, based on Y, and the other two characters show a reasonable degree of correlation with S. The curve of Y for VII B does not resemble at all that of S, unlike all the other populations, so it is probable that the seed and perianth size are less well correlated with the congestion index than they usually are.

Figure 96 is a scatter diagram of seed size : perianth size for VII A; different symbols are used to represent values of S below and above 30. The two characters plotted show a positive correlation, and the higher values of these are correlated with the plants having S greater than 30, the lower values with S less than 30. A similar diagram for VII B shows a complete lack of correlation between the characters (fig. 97). There is no correlation between s x w and P, and the two groups of S are scattered at random throughout the diagram.

These correlations can be expressed by the correlation coefficient, and are calculated from the formula:-

$$r = \frac{\frac{1}{N}\,\sigma\,(x-\bar{x})(y-\bar{y})}{\sigma_x\,\sigma_y}$$

where N is the number of pairs of characters, $\bar{x}$ and $\bar{y}$ the means, and σ_x and σ_y the standard deviations of each character.

A perfect positive correlation will have r = +1, and a perfect negative correlation, r = -1. No correlation at all will have r = 0, and partial correlations will range from 0 to + and - 1.

The correlation coefficients were calculated for each pair of characters making up Y for both VII A and VII B, and are summarised in the table below:-

	r	
	VII A	VII B
s x w and P	+ 0.505	+ 0.119
S and s x w	+ 0.62	- 0.146
S and P	+ 0.648	- 0.264

The table shows that VII A has all the characters with a positive correlation between 0.5 and 0.65, which is not a particularly high degree of correlation, but it is at least significant. The degree of correlation of the characters in B displays a completely different picture, two of them being negative, and one positive; none of them exceeds 0.3.

The lack of correlation suggested by the lack of similarity of the ogives of S and of Y in VII B, and demonstrated in the scatter diagram (fig. 95), can therefore be assessed mathematically, and can be compared with the relatively normal population VII A, which shows a good positive correlation of all three characters.

That the "intermediate" nature of the ogive of Y is caused by the lack of correlation between the characters can be proved, as shown above, but it is not so easy to demonstrate the cause of the lack of correlation. The use of the congestion index alone would give two groups of plants, with congested and lax inflorescences, but when the other characters are superimposed the two groups merge into one; the point to be decided is which of these gives the most realistic representation of the structure of the population.

As was mentioned above, a large number of plants in VII B had only one seed in each ovary, instead of the normal three; in many cases only a few flowers in the inflorescence had set seed at all. None of the plants was completely sterile, but there was certainly a significant reduction in fertility of a considerable proportion of the population. Pollen fertility could not be examined, because the plants were collected when the seed was ripe, and all the pollen had been shed. This reduction in fertility, combined with the lack of correlation of the characters in the Y index, leads to the conclusion that this group of plants may well contain a high proportion which are of hybrid origin, as well as plants of both <u>multiflora</u> and <u>congesta</u>. The seeds from this

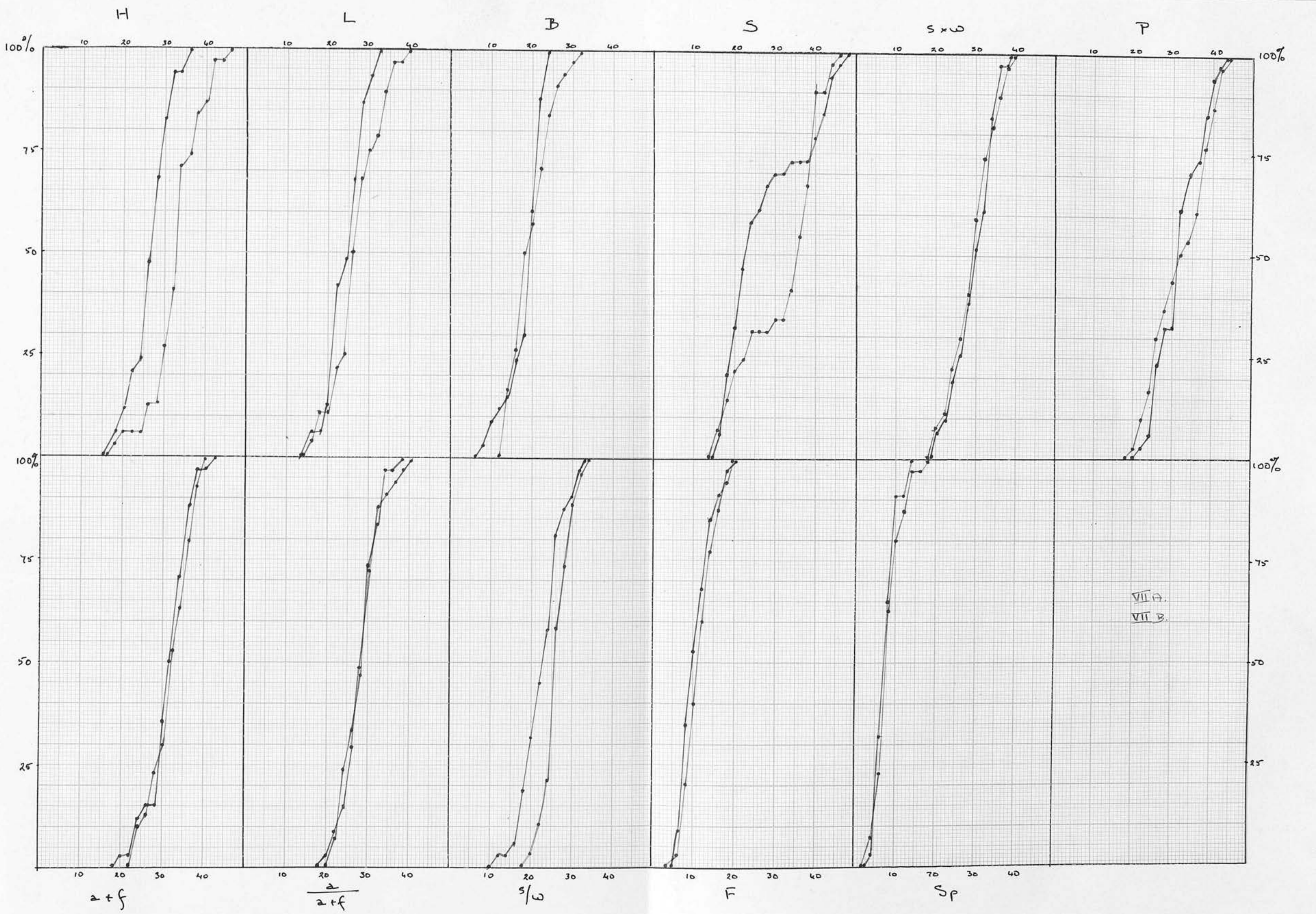


Fig. 95. Ogives of the diagnostic characters in VII A and B.

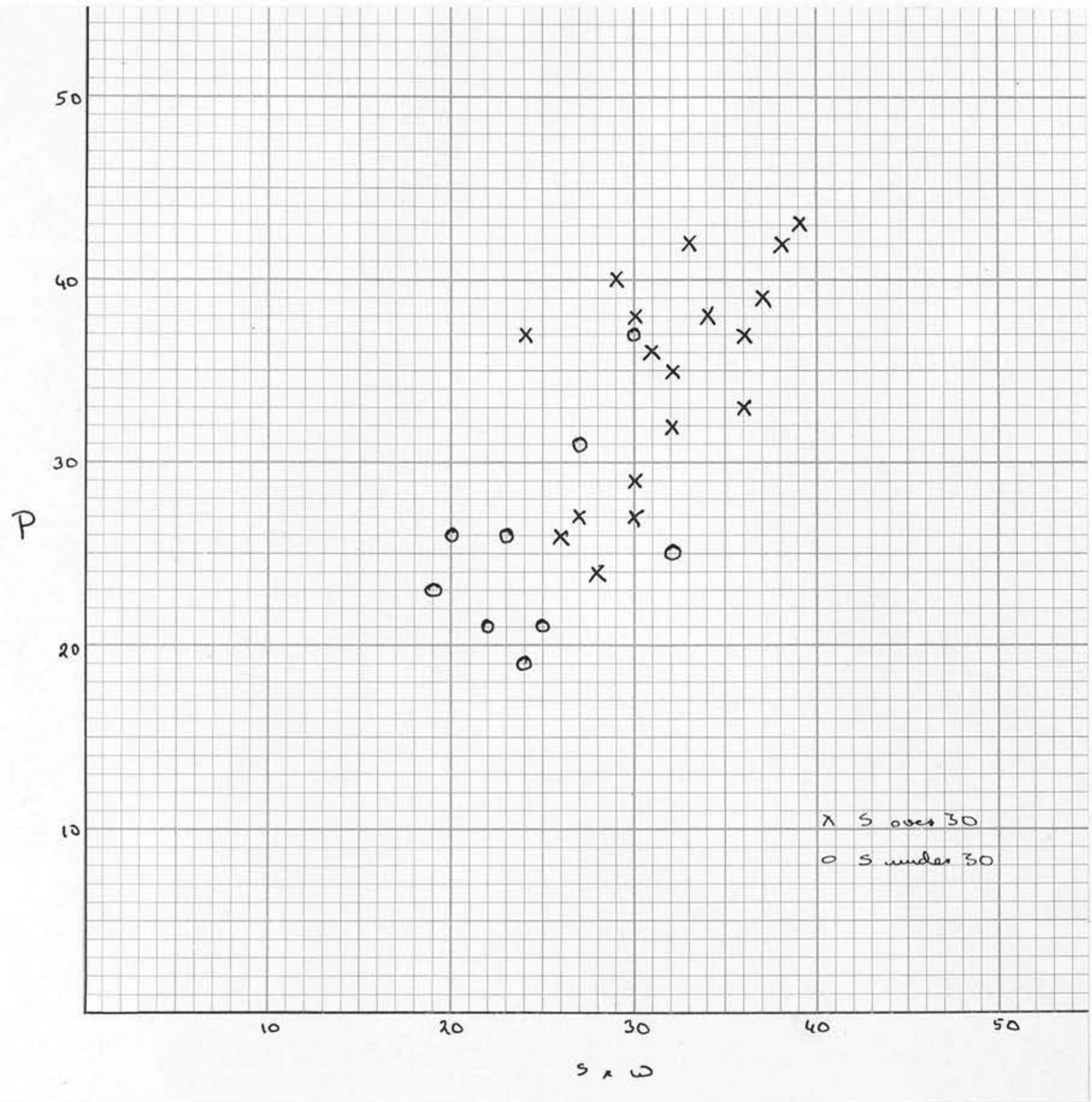


Fig. 96. Scatter diagram of s x w and P, with S superimposed, for VII A.

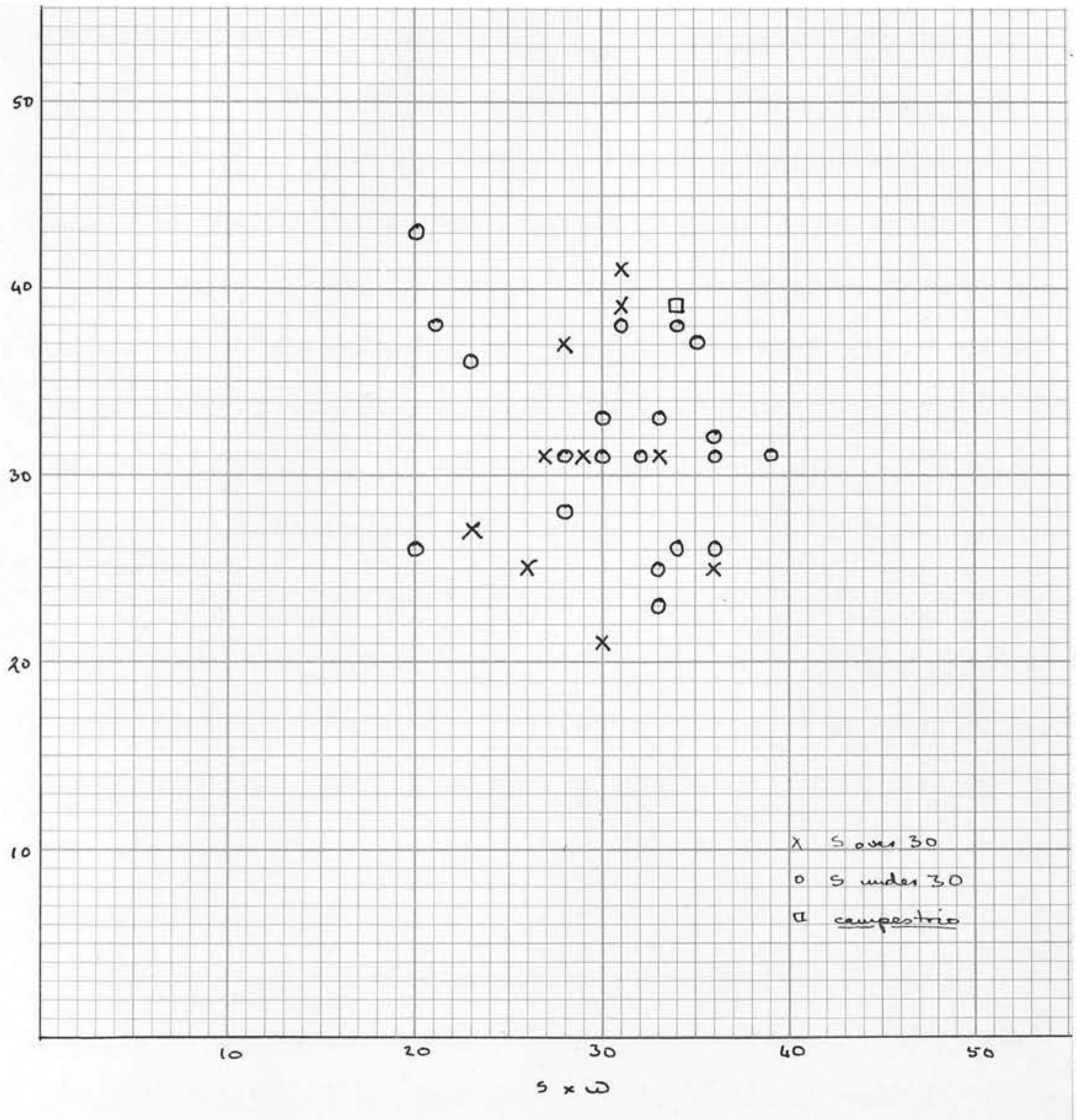


Fig. 97. Scatter diagram of s x w and P, with S superimposed, for VII B.

population were viable, and showed a germination of 80% when grown on filter paper, and 88% in soil, which was about 10% less than normal, but presumably not sufficient to have much effect on subsequent generations of the plants.

It seems that, in this case, the use of the index does give a more accurate interpretation of the population than the use of S alone. Although the latter divided the plants into two groups, and therefore makes it easier to give a name to the individual plants, the lack of correlation with the other two characters leads one to doubt the existence of two distinct groups in this population (VII B); VII A is much more like all the other populations studied, and can be divided into two groups, either by the Y index, or by the degree of congestion of the inflorescence.

Conclusion.

The relationship of congesta and multiflora in the field is shown to be one of co-existence in the same habitat, without the complete mingling of the two taxa. Only in one of the populations, VII B, does the number of intermediate forms exceed the number of plants of multiflora or of congesta. All the other populations show a bimodal distribution of the Y index, and a very strongly bimodal distribution of the congestion index (S).

The general pattern of population structure is of one taxon predominating, with varying proportions of the other, and of intermediate forms, contained within it. The number of intermediate plants present does not seem to vary much with the two taxa, although the more closely they approach equal numbers of each, the more frequent the intermediates seem to be. Where the population is about 90% of one taxon, with only a few plants of the other, intermediates are rare.

In conclusion, multiflora and congesta seem to be capable, under suitable conditions, of producing a hybrid population, but this rarely happens, and they are most frequently found growing side by side without the establishment of more than a few possible hybrids in each population. There must therefore be at least a partial internal barrier to crossing, which allows the two taxa to preserve their separate identities in the field, despite close proximity to each other.

I. PLANTS GROWN IN CULTIVATION.

The performance of the twelve gatherings (3 each of multiflora, congesta and campestris, and 3 of the first two mixed) was discussed at the end of chapter IV. The plants were also used to determine whether or not the characters used to distinguish the taxa in the field were stable, and that the differences between the groups were maintained when the plants were grown under cultivated conditions in the experimental garden.

The inflorescences from these plants were cut off as close to the base as possible, so that the maximum height could be obtained. As with the wild plants, the inflorescences were collected when the seed had set, and they were dried and later measured in the laboratory in exactly the same way. The tallest inflorescence in each plant was again chosen, as with the wild plants, to make the measurements as nearly comparable as possible. The data obtained were treated in the same way as those from the population studied, and the three indices were worked out as before.

A comparison of the different sets of characters shows that the relationships found in the field are maintained under cultivated conditions. Figure 98 shows ogives of the various characters used. The variation of each character is shown for each of the four groups of plants grown. Figure 99 shows the mean and the range of variation of the wild plants compared with those of the cultivated plants. The range of the latter is very much less than that of the former in each case, which is only to be expected, since there are only about 15 plants in each cultivated group, compared with 150 to 500 in the wild ones. The differences of the means are much less than those of the maxima and minima.

Stem Height.

The range for campestris is very small, but the means (17 and 18) for the wild and the cultivated plants vary only a little. Multiflora, on the other hand, again shows a very small range, but the means differ by about 6 units, the cultivated plants being considerably taller than the wild. In congesta the opposite is the case, and the cultivated plants are smaller than the wild. The result of these differences is a reversal of the relationship of multiflora and congesta shown in the field, where the latter was taller than the former; when the plants are cultivated, congesta is considerably smaller than multiflora. Campestris maintains its position in relation to the other taxa, and the range of its height does not overlap at all those of multiflora and congesta.

The change in the relationship of multiflora and congesta is probably because of the conditions under which they were grown. These conditions suited multiflora well, but the soil was somewhat dry for congesta, which has been shown in chapter IV to prefer moister, more boggy habitats than multiflora. The lack of moisture probably prevented congesta from reaching its maximum height, while multiflora grew relatively well. It may be, on the other hand, that the plants of congesta grown were genetically shorter than those of multiflora, as they are both well within the ranges of variation of the wild plants.

The _congesta_ plants did not flower or set seed so well as _multiflora_ (see Ch. IV), and appeared generally to be less resistant to the dry conditions which prevailed in the early part of 1956, so that the first explanation seems the more likely.

Leaf Length.

The mean leaf length of _campestris_ is more or less the same in the wild and the cultivated plants, but the means of both _multiflora_ and _congesta_ are higher in the cultivated groups. The increase in _multiflora_ is much greater than that in _congesta_, so that the mean of _multiflora_ is higher than that of _congesta_ when cultivated, although they are about the same when wild.

Leaf Width.

Campestris is again more or less the same when cultivated and wild, but _multiflora_ shows a considerable increase in the width of the leaf, and the maximum even exceeds that for the wild plants; the mean is about 8 units higher in the cultivated plants than in the wild. _Congesta_ shows a slight increase, but this is much less than in _multiflora_, and the mean is lower.

Stamen Length.

The ranges are again much less. The means of the wild and cultivated _campestris_ are more or less the same, but in _multiflora_ and _congesta_ the means of the cultivated are lower, but the ranges of variation are well within the range of the wild.

Anther: total Stamen Ratio.

The relationships are more or less the same as in the previous character, campestris and multiflora being much the same wild and cultivated, but congesta, having a slightly lower mean when cultivated than when wild.

Seed Length:Width Ratio.

In campestris the means are the same, but both congesta and multiflora have higher means when cultivated, especially the former (this may have been caused by the failure of some of the seeds to ripen properly).

Number of Heads per Inflorescence.

There was an increase in the average number of heads in each inflorescence of all the taxa when cultivated.

Number of Flowers per Inflorescence.

This character was not measured, as the inflorescences were collected rather late, and were dry and brittle when preserved, so that numbers of flowers fell off before a count could be made.

Congestion Index.

The means of the wild and cultivated plants are about the same in campestris and congesta, but the range of the latter when cultivated is exceedingly small. In multiflora the mean is lower when cultivated, indicating a more lax inflorescence.

Seed Size.

Campestris is again more or less the same wild and cultivated, as is multiflora, but the seeds of congesta are considerably smaller when the plants are cultivated, and the range fell in the lower half of the wild range. The seeds may not have reached their full size owing to the dry conditions.

Perianth Size.

The mean size of the perianth of the cultivated campestris is very slightly less than that of the wild. In multiflora it is also slightly less, and in congesta it is slightly more, so that the difference between congesta and multiflora in this character is greater in the cultivated plants than it is in the wild.

These comparisons show that the differences in height, and in the length and width of the leaves between campestris, and multiflora and congesta are real, and are presumably genetically controlled. The analysis of the wild plants showed that congesta was significantly larger in the vegetative characters than was multiflora; when samples of these taxa were grown in cultivation, the situation was reversed. This reversal indicates that the differences in height between the taxa probably result from the different habitats in which they grow. To determine the exact nature of these differences in size, it would be necessary to grow the two taxa together in a complete range of habitats, from a relatively dry, light soil, to a completely saturated, boggy one; some variation in the amount of shade might also have an effect on the height of the plants. The vegetative characters distinguishing campestris from multiflora and congesta are therefore of some taxonomic importance, while the slight differences between the two latter are not.

The comparison of the floral characters shows few significant differences when the plants are cultivated. There is a tendency for all the taxa to have more heads in the inflorescence when cultivated, and also to have more inflorescences on each plant, but the relations between them remain the same. The characters which show great differences in the means are 1) the congestion index for multiflora, where the mean is very low in the cultivated plants because the individual stalks grow longer, reducing the value of S, and 2) the seed size of congesta, which is less in the cultivated plants than it is in the wild; this difference is due mainly to one gathering, which had exceptionally small seeds for congesta, and it may also be due to cultivated conditions.

The X, Y and Z indices were worked out for the cultivated plants in the same way as for the wild ones. Since the number of flowers was not counted only four characters were used to make up the X index, which is therefore correspondingly slightly lower.

The means and ranges of variation of the indices are shown in figure 100, and in figures 101 and 102 the ogives of the three indices for each group are shown.

Figure 100 illustrates the relationships of the four groups to each other. In the Z index campestris has a far lower value than the other three taxa, and is quite distinct from them; in the wild populations the ranges overlap. When the plants are all grown under the same conditions the index of the vegetative characters is just as good for separating the _campestris_ group from the others as is the index of the floral characters (X). The highest mean of Z is in _multiflora_ (99.9); _congesta_ is considerably lower (85.9), and the mixed populations come in between with a mean of Z = 94.7.

The X index shows a somewhat similar relationship, with _campestris_ well separated from the other groups. The mean of _campestris_ is X = 60.25, and those of _multiflora_ and _congesta_ are 103.7 and 99.9 respectively; the mean of X for the mixed population is 94.3, lower than either _multiflora_ or _congesta_. Figure 99 shows that this group has lower values of all characters other than the number of heads in the inflorescence, compared with _multiflora_ and _congesta_. This may be due to the mixed nature of the gatherings, and to the presence of possible hybrids within them; resultant sterility, or partial sterility of the seeds or stamens might bring about a change in the size or shape, which would alter the ratios involved. This seems somewhat unlikely, as the degree of sterility appears not to be very great, and the differences are not large enough for it to be impossible to account for them by the normal variation between populations. The X index, even without the number of flowers, when calculated for the cultivated plants shows that the difference between _campestris_ and the other taxa is even greater than when the plants are grown in their natural habitats.

The Y index shows no overlapping between the ranges of _multiflora_ (mean 55.5) and of _congesta_ (mean 98.6), and the two groups are as well separated from each other as campestris is from them both by X. The campestris group has a mean of 78.4, intermediate between multiflora and congesta; the range overlaps that of the latter only slightly and of the former not at all. The mixed populations have of course a much wider range (Y = 52 - 102) than either multiflora or congesta, but it does not extend to the maximum value of congesta, or to the minimum of multiflora. The mean is 77.7, and is in part of the range where no plants occur, and is therefore hardly significant. The ogives for the group (fig. 101b) show that Y has a bimodal distribution, and that there is a gap between Y = 75 and Y = 85; the means of the two parts of the mixed populations can be estimated from the graph, one having a mean of Y = 65, and a range of 52 - 75, the other having a mean of Y = 93, and a range of 88 - 102. These means compare with 55.5 and 98.6 respectively for multiflora and congesta, and are thus higher than the first, and lower than the second. The range of the lower part of the group is larger than that of multiflora, and extends well above it, but the range of the upper part of the group is less than that of congesta.

The Y index shows that pure multiflora and congesta are well separated, and that the mixed populations can be split into two groups which are less well separated, but are still distinct.

Figure 103 is a scatter diagram of X and Y for all the cultivated plants. Different colours are used for campestris, multiflora and congesta and for the mixed populations, and different symbols are used for the populations within each group.

The three groups are quite separate from each other, and there seems to be no morphological intergradation. The mixed gatherings are split between congesta and multiflora. The different gatherings of campestris show no grouping together, and show a more or less random distribution, but in multiflora and congesta there is a tendency for the plants in the same gathering to be relatively close to each other in the diagram. The plants of Davis 68 all have rather low values of Y, and high values of X, while Buchanan 1b is high for both X and Y. Henderson 17 seems to be split into two groups on the X index, because three of the plants had rather large anthers, which gave a low value of a + f, and also lowered $\frac{a}{a + f}$.

The diagram shows that while the mixed gatherings fall into either multiflora or congesta, and some of the plants are well within the groups (particularly in congesta), four of them are in an intermediate position, although nearer to multiflora.

The morphological study of the plants under cultivated conditions shows that the distinctions between the groups revealed by the study of herbarium material, and the investigation of mass gatherings of wild plants are maintained, and even accentuated. This is particularly true of the vegetative differences between campestris and the other taxa. Vegetative differences between multiflora and congesta are probably environmental, but the response to identical growth conditions of the two taxa differed, so that a physiological distinction between them is indicated. Multiflora and congesta are about as distinct from each other in the pure populations as they are from campestris; the inclusion of mixed populations about halves the difference between the ranges, but the groups still appear to be quite distinct.

J. SUMMARY AND CONCLUSIONS.

The characters used to separate the three taxa, campestris, multiflora and congesta, were analysed for a large sample of over 1000 plants, from about 50 populations. The range of variation of each character for each taxon was worked out.

It was found that the eleven diagnostic characters used could be combined together to give three indices which could be used to separate the taxa. The first of these indices, the Z index, is a combination of the three vegetative characters, H, L and B. This index can be used in most cases to separate campestris from the other taxa, but the differences between multiflora and congesta are only slight in this respect, and cannot be used taxonomically.

The second index, the X index, is a combination of the five characters which separate campestris from multiflora and congesta : $a + f$, $\frac{a}{a + f}$, s/w, F and Sp. This index can be used with a considerable degree of accuracy, and relatively few intermediate values are found.

The third index, Y, is made up of the three characters in which multiflora and congesta differ : S, $s \times w$ and P. The separation into two groups in this case is rather less perfect than in the case of X, but the majority of the plants can be assigned to one or other of the taxa. The proportion of intermediate plants is, however, higher than it is with the X index.

The best character for separating multiflora and congesta is the congestion index, S. To give this character greater weight, a discriminant function was applied to the Y index; this resulted in a far better separation into two groups, but it appears that the first treatment may be closer to the natural relationships of the plants, and that the rather high proportion of intermediate plants may be composed of at least some plants of hybrid origin.

Twelve samples of plants grown in the garden showed that the characters used to distinguish the plants in the field were maintained under cultivated conditions, although the relationship of multiflora to congesta in the vegetative characters was reversed; all the floral characters remained much the same. The range of variation of all the characters was much less for the cultivated plants than it was for the wild, but the sample was so much smaller that little significance could be attached to the fact. Three samples were of multiflora and congesta mixed, and while some of these plants fell within the range of variation of the taxa, others occupied a more intermediate position, although they were nearer to multiflora than they were to congesta.

All the evidence from the wild and the cultivated plants indicates that campestris can be easily separated morphologically from the other taxa, both by vegetative and by floral characters. It is also shown that about 90% of the remaining plants can be assigned to either multiflora or to congesta, while the 10% which occupy an intermediate position may be in fact of hybrid origin.

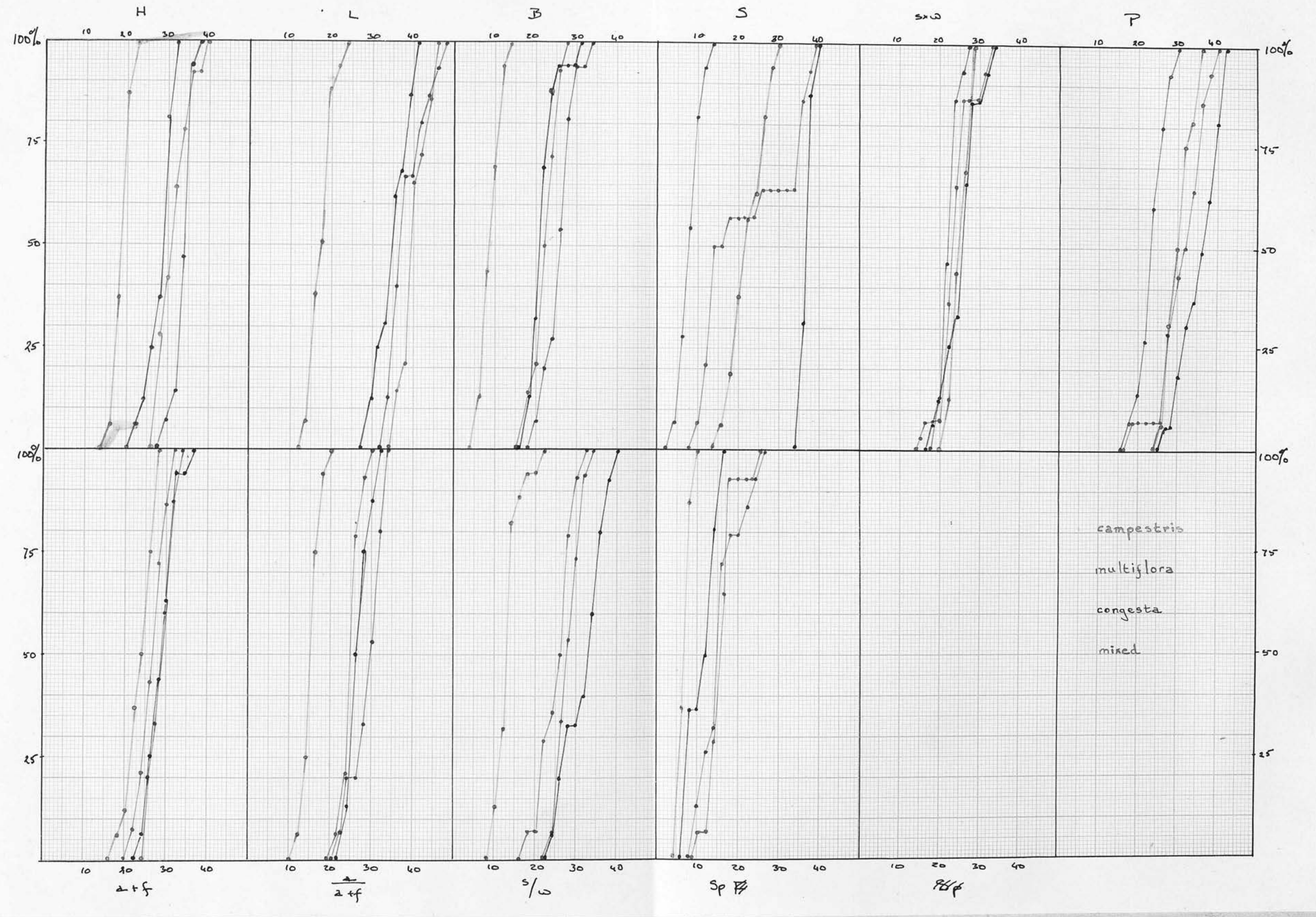


Fig. 98. Ogives of the diagnostic characters for the cultivated plants.

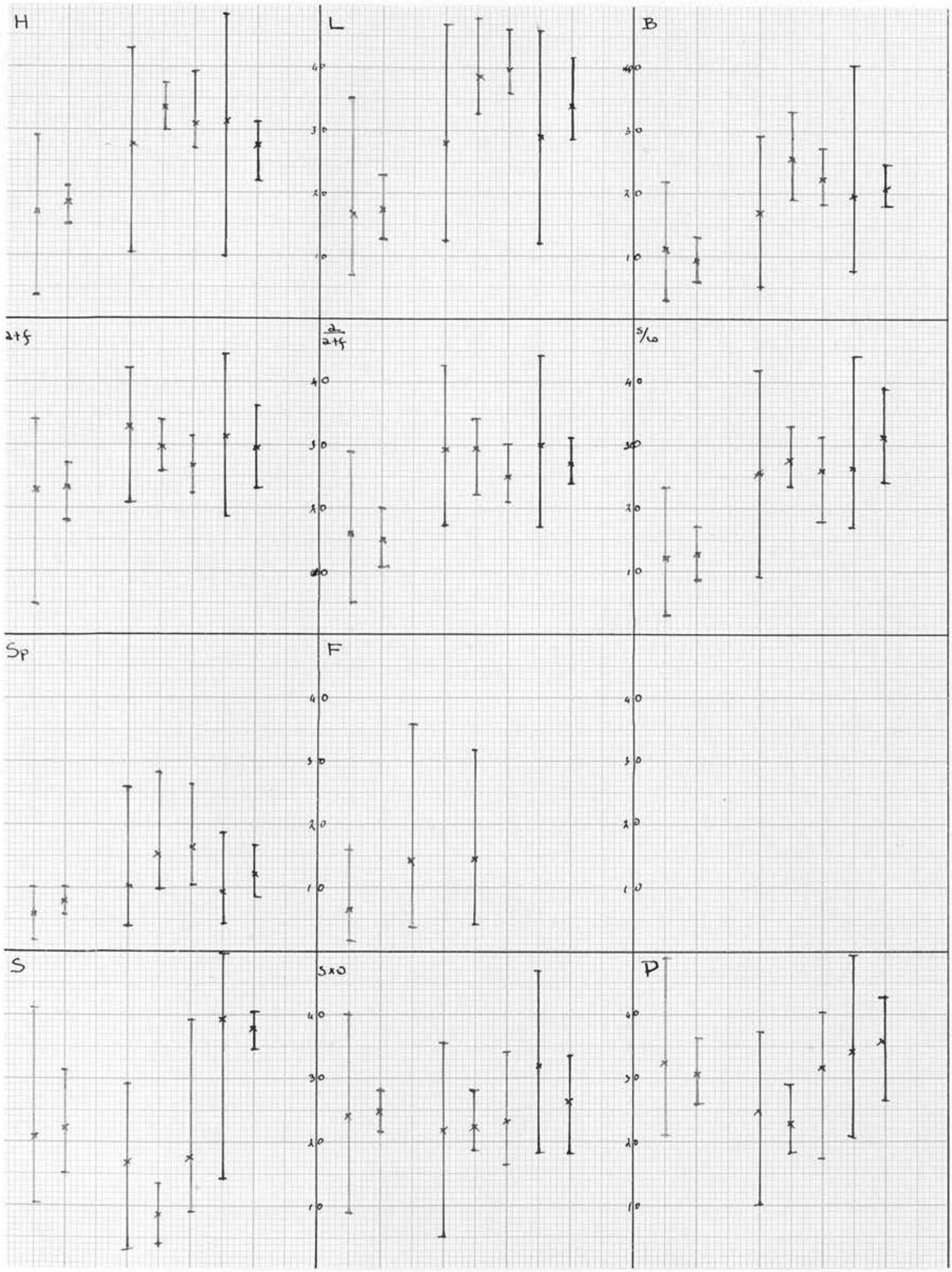


Fig. 99. Range and mean of the diagnostic characters of the wild and cultivated plants; <u>campestris</u> green, <u>multiflora</u> red, <u>congesta</u> purple and mixed (cultivated) blue.

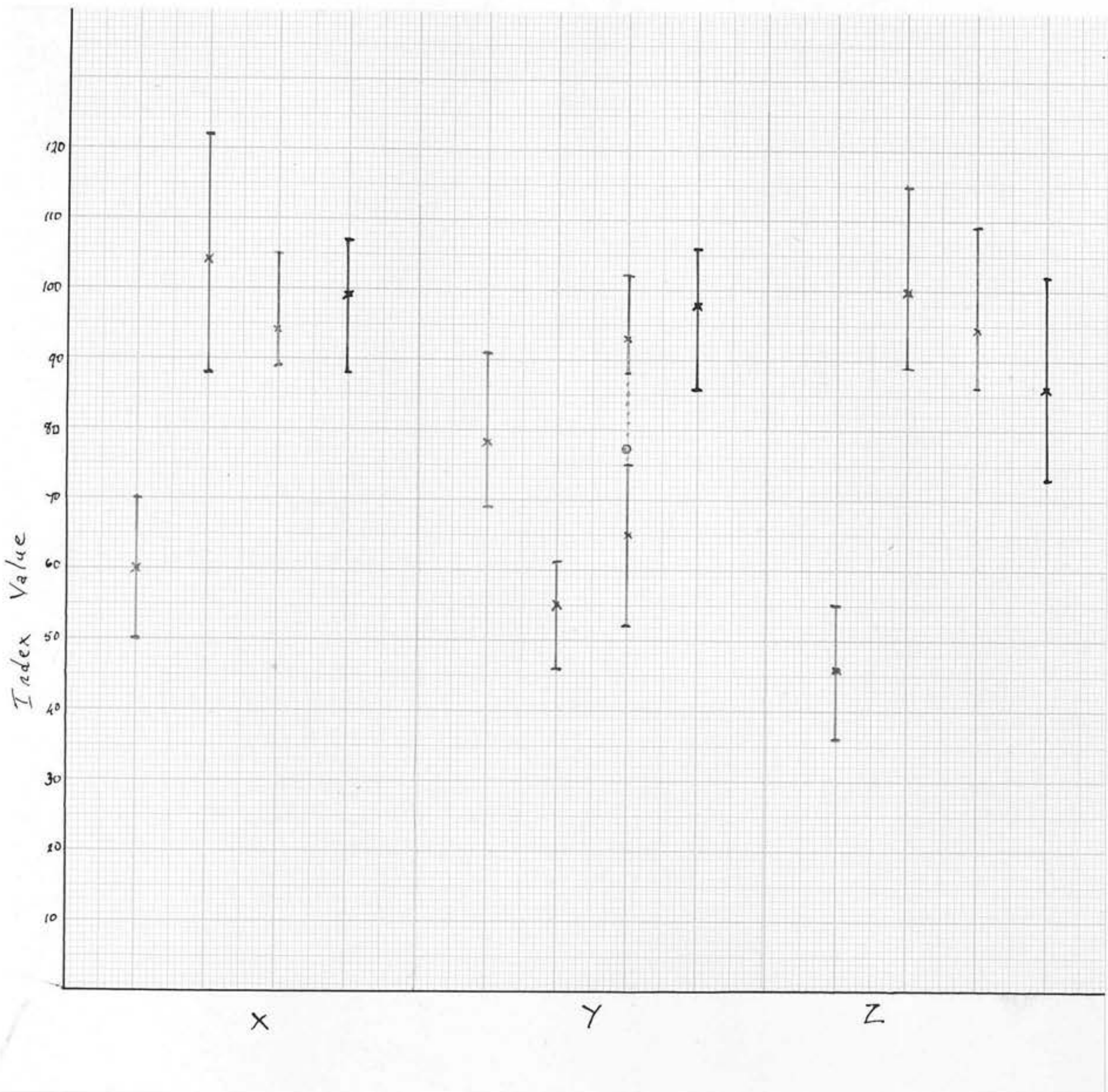
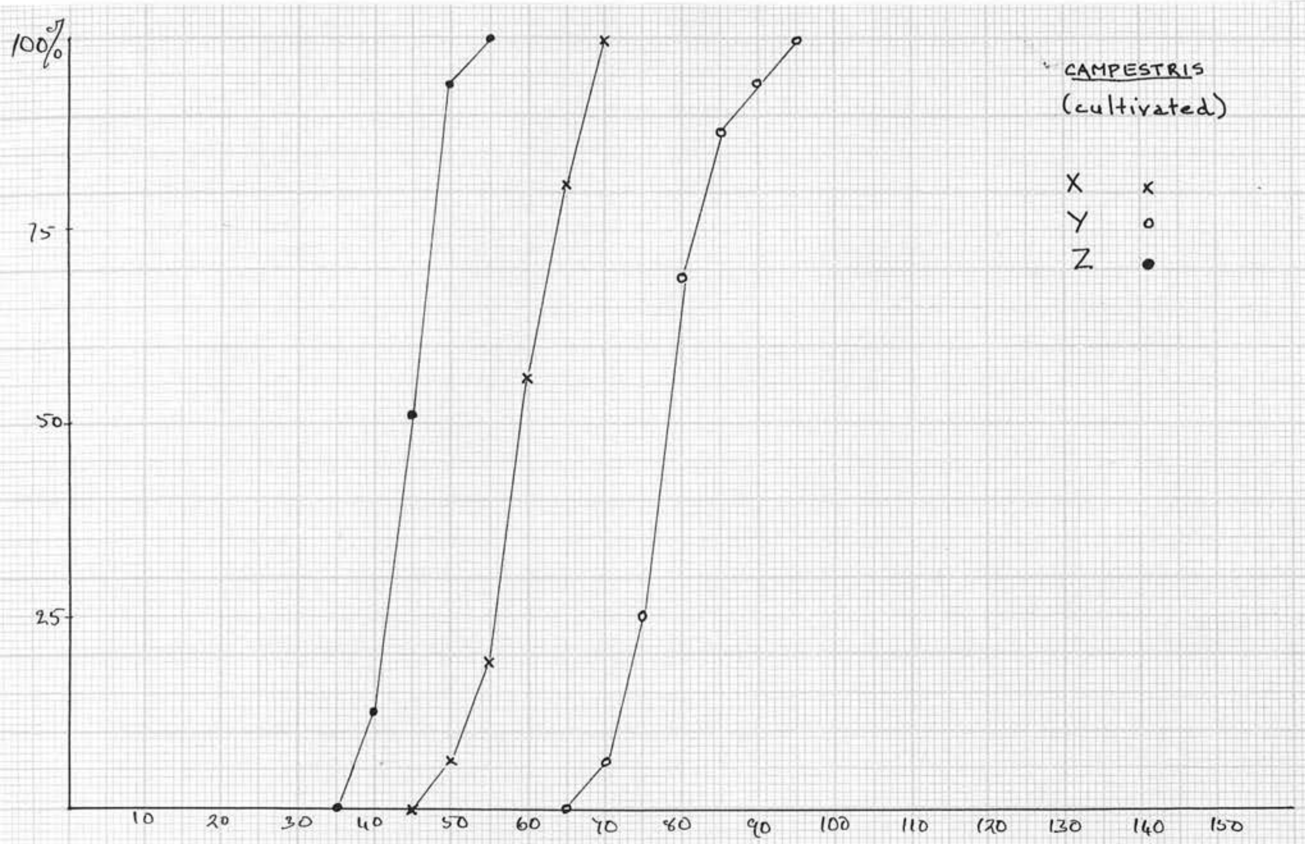


Fig. 100. Range and mean of the indices of the cultivated plants.



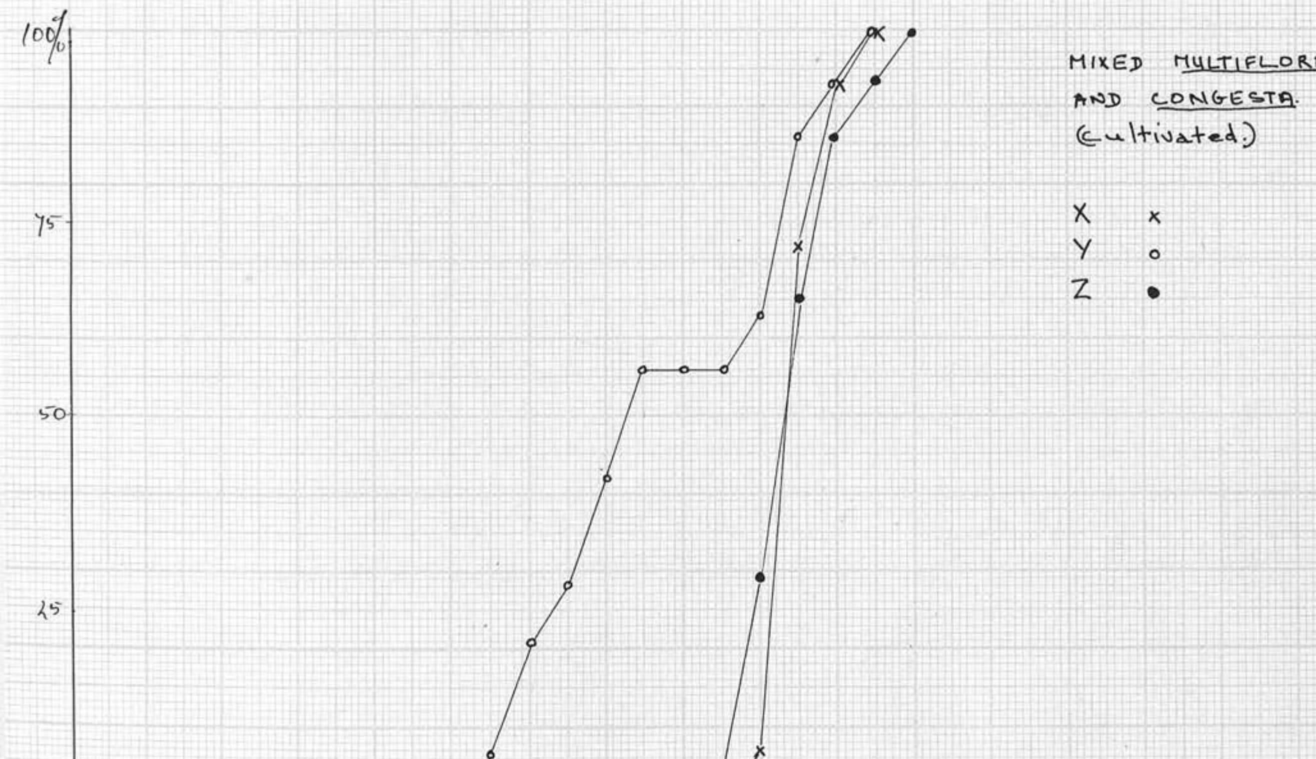


Fig. 101. Ogives of X, Y and Z for <u>campestris</u> and the mixed gatherings of cultivated plants.

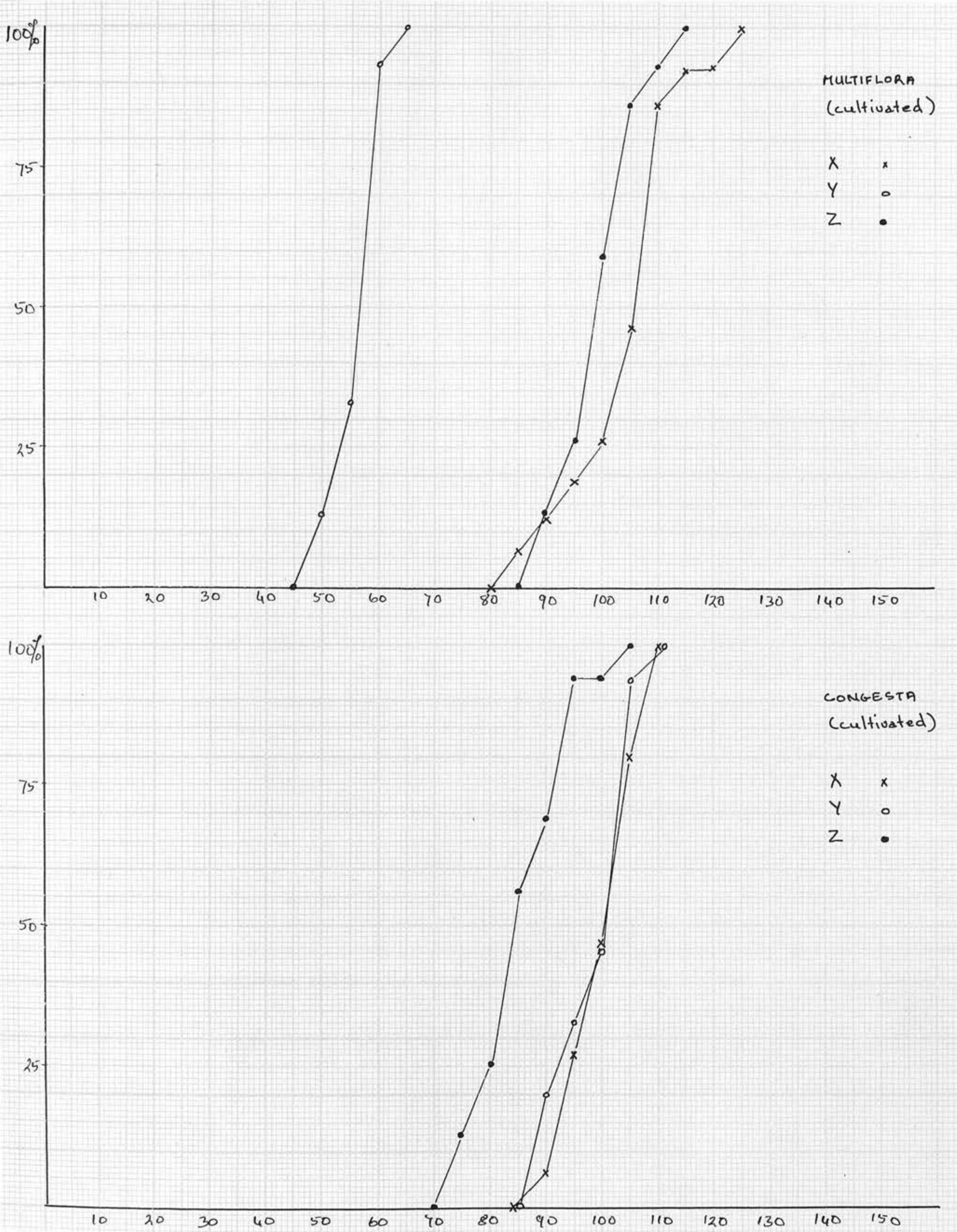


Fig. 102. Ogives of X, Y and Z for cultivated multiflora and congesta.

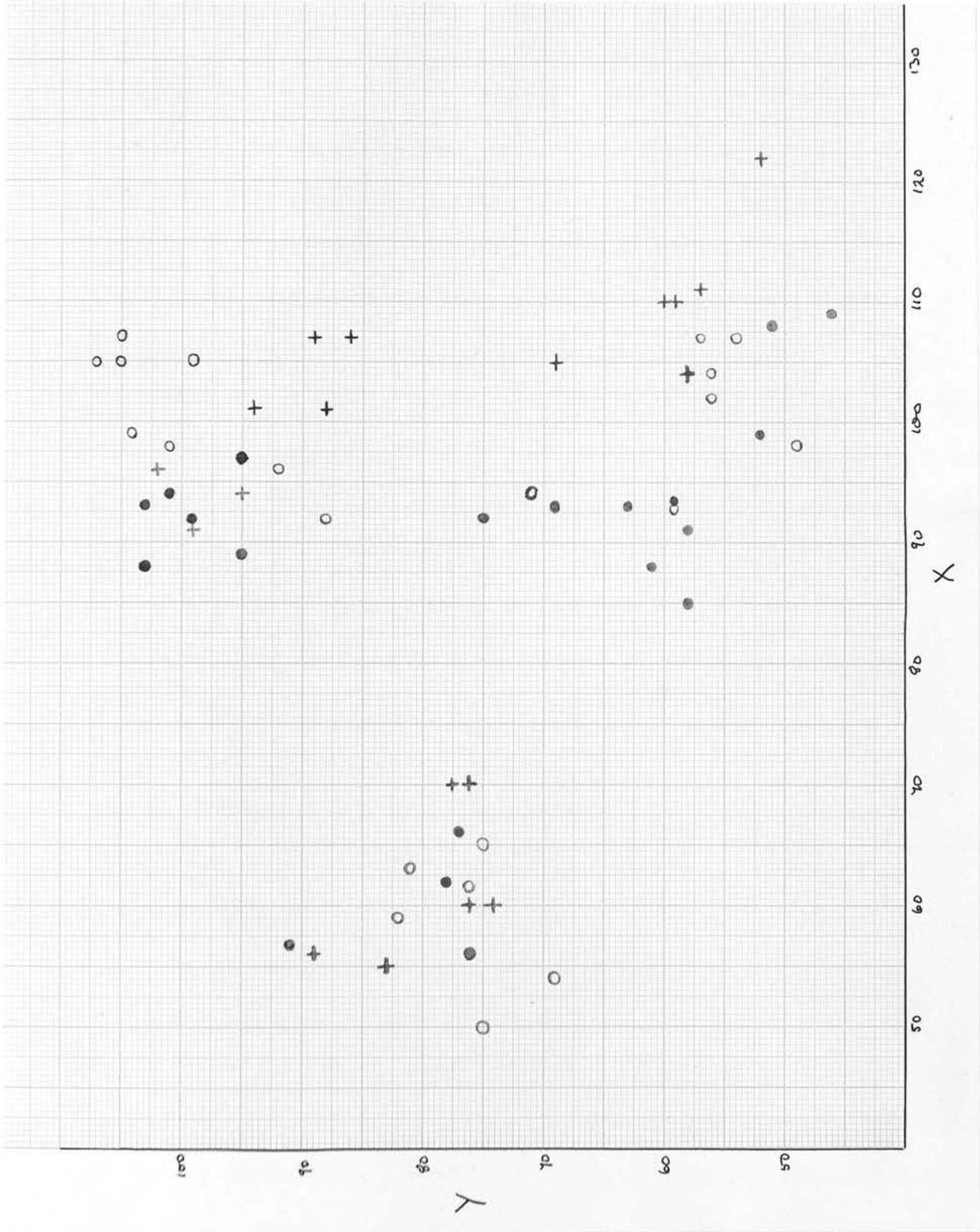


Fig. 103. Scatter diagram of X and Y of the cultivated plants, showing the samples from which they came.

VI CYTOLOGY.

The chromosome numbers of various species of Luzula have been counted by different workers [Darlington & Wylie, 1956; De Castro et al., 1949, 1950, 1954, 1956; Gardé, 1950, 1952; Nordenskiold, 1949, 1951, 1956; etc.] The basic haploid number in the genus is 6, although L. purpurea, the only annual species in the genus has n = 3.

Nordenskiold (1951) showed that there are two types of polyploidy: normal, where both the number of chromosomes and the amount of chromatic material are doubled, and whay Nordenskiold calls "endo-nuclear" polyploidy. In the latter case the number of chromosomes is doubled, but the amount of chromatic material remains the same. The type of polyploidy is brought about by the fragmentation of the original chromosomes, so that the higher the chromosome number, the smaller are the individual chromosomes.

It is thought that this fragmentation is made possible by the peculiar nature of the centromere, which, instead of being localised on a particular part of the chromosome, is diffuse, and extends along the whole, or most of the length of the chromosome. Much work has been done on the purely cytological aspect of this phenomenon in Luzula [Brown, 1954; Battaglia, 1955; Berger, 1949: De Castro et al., 1949, 1950, 1954, 1956; La Cour, 1953; Östergren, 1949; Thomas, 1950], but only Nordenskiold (1951 and 1956) has made any serious attempt to correlate the cytological results with the taxonomy of the genus. In some of the papers where L. campestris is cited one is not quite certain exactly which member of the species complex was being used.

Nordenskiold has treated all the different taxa with which she has worked as distinct species, except for L. multiflora var. lutescens from Japan. She does, however, recognise the existence of a complex of species related to L.campestris, and her most recent paper (1956) consists of a detailed examination of this group of taxa, which she calls the "Luzula campestris species complex". In this paper Nordenskiold gives chromosome counts for various taxa in the group, collected from widely separated localities in Europe, America and Asia. She also gives the results of hybridisation experiments carried out between the different taxa. She finds that more successful crosses are obtained between taxa at the same level of polyploidy, even if they are geographically separated, than between taxa at the different levels of polyploidy. Most of the taxa seem to form a normal polyploid series, but a few (e.g. sudetica, $2n = 48$) are endo-nuclear polyploids. These she considers at the appropriate level of ploidy, depending on the number of chromosomes and their size; sudetica is considered to be at the diploid level, as there are 48 very small chromosomes, resulting from the original 12 chromosomes having fragmented twice.

The present study is concerned more with the morphology of the campestris group, and with the structure of the wild populations in Britain, than with the purely cytological problems, interesting though these are. Investigation of the chromosome numbers was carried out to supplement the morphological studies, and to add to the evidence of ecology, geographical distribution and morphology in an attempt to define the taxonomic status of the plants. Some of the other species found in Britain were also counted, and the results are summarised below.

Table 11.

	2 n
L. sylvatica	12
L. luzuloides	12
L. pilosa	c. 60
L. forsteri	24
pallescens	12
campestris	12
multiflora	36
congesta	48
? hybrids	30, 42

A. MATERIAL AND METHODS.

Various stains and mountants were used in the preparation of the cytological material, all associated with a squash technique. Nordenskiold states (1951) that she used root tips fixed in acetic-alcohol, and stained with aceto-carmine. This method gave results, but more satisfactory preparations were obtained by using other growing parts of the plant, and by staining with acetic-orcein instead of carmine.

1. Root Tips.

The plants were grown in a light sandy soil, in small pots which were kept in a cold frame. The roots were cut off about

0.5 cm. from the tip, and were fixed for 24 hours in 1 : 3 acetic-alcohol. Pre-treatment with 0.2% colchicine, or with a saturated solution of α-monobromonaphthalene appeared to have little effect. Staining was by aceto-carmine or by acetic orcein squash techniques. The root-tips are very small, and the number of cells dividing at one time is also small. The cytoplasm in the cells of the root tip tends to stain deeply, and it is not easy to obtain a satisfactory squash preparation using this technique, even when concentrated hydrochloric acid is added to the orcein to aid maceration.

2. <u>Leaf Bases</u>.

Living plants were not obtained from most of the populations studied, so that a direct comparison of the morphology and the chromosome number was not possible in most cases. The plants were, however, in fruit when they were collected, and a good supply of ripe seed was available.

The seedlings were grown in petri-dishes on damp filter-paper, or in a germinating tank, at room temperature. The roots first appear in a week to ten days, and the first leaves some days after that. The plants were left until the second true leaf had appeared. Whole seedlings were pre-treated for 2 - 3 hours in a saturated solution of α monobromonaphthalene, rinsed, and then fixed in 1 : 3 acetic alcohol for 12 - 24 hours. For the stain, a solution of 1% orcein in 45% acetic acid was used, with 1 ml. conc. H Cl added to every 10 ml. of the stain.

Several drops of the stain were placed in a watch glass, and a whole seedling immersed in it. The watch glass was then heated over a spirit lamp until the stain was nearly boiling, and it was then left for at least 10 minutes. The seedling was then removed from the stain, placed on a clean slide, and the basal, growing part of the leaves was dissected off and placed in a drop of fresh stain on another slide, where it was teased out as far as possible with dissecting needles. A filmed coverslip was placed in position, covered by a pad of blotting paper, and pressed firmly. The H Cl in the stain provides sufficient maceration for the cells to separate reasonably well, although they do tend to adhere together in lines along the length of the leaf. The cells can be separated further by the application of localised pressure on the cover-slip with the point of a dissecting needle, but care must be taken not to crack the cover-slip in the process.

3. <u>Ovary Walls</u>.

During an attempt to obtain pollen mother cells from mature plants grown in the garden, the very young developing ovary was used to make a squash preparation. At this stage the ovary walls are growing rapidly, and numerous mitotic cells are available. The flower buds were fixed in 1 : 3 acetic alcohol for 12 to 24 hours. The perianth and anthers were removed from around the ovary (the latter being sometimes used on another slide); the ovules were dissected out so that there was no chance of haploid cells being included in the preparation; the stigmas were also removed. The ovary wall was then placed in a drop of aceto-carmine on a slide, and teased out into small pieces until the cells were becoming obviously stained. A filmed cover-slip was put in place, and excess stain removed with blotting paper. The slide was heated several times over a spirit lamp until the required intensity of staining was obtained, and pressure was then applied to the cover-slip to separate the cells further.

Acetic orcein squashes were also used for this material; the whole flower bud was heated in the stain, the ovary then removed and treated as before. On the whole it was found that the aceto-carmine technique gave better results with this material than did the orcein.

4. Pollen Mother Cells.

There was considerable difficulty in obtaining satisfactory results from the pollen mother cells in Luzula, and the only reasonable preparations were secured after the main part of the work was done. The haploid numbers are therefore not included in the tables of the chromosome numbers.

In the first attempts the whole flowers or inflorescences were fixed in 1 : 3 acetic alcohol, and anthers at varying stages of development were removed and stained in aceto-carmine. No good results were obtained. Later attempts used fresh material, which was not fixed at all. An anther was dissected off the flower, placed in a drop of aceto-carmine, and the pollen mother cells or developing pollen grains squashed out. If the inflorescences are kept in a jar of water in the laboratory, or the plants grown in pots indoors, then it is possible to obtain the anthers at some stage of active division, and a number of quite good preparations were made in this way.

The chief drawback to this method was the fact that in Luzula, as in the rest of the Juncaceae, the pollen is shed in tetrads. In all the preparations obtained by this method the pollen grains had developed, and the nuclei were at the stage of dividing to give the tube and generative nuclei. If earlier stages, the first division of the pollen mother cell, had been obtained this difficulty would not have arisen; it will no doubt eventually be eliminated by further improvements in technique.

Mounting Media.

Since the number of cells dividing at one time is never very large, the risk of losing them when making a permanent preparation was too great, and various methods of making permanent and semi-permanent preparations without removal of the cover-slip were tried.

The quickest and simplest method is simply to seal the edges of the cover-slip with Gurr's Laktoseal or some similar substance, and leave the cells mounted in the original stain. The preparations lasted quite well for a week or two before drying out, but the stain tended to become rather intense. By this method a fairly large batch of slides could be made in one day, but they all had to be examined within the following two weeks.

Another method of making a semi-permanent preparation is that of Rattenbury (1956); the squash is made as before, and the preparation is first irrigated with a drop of 45% acetic acid to remove the excess stain, and then with a drop of 10% glycerine in 45% acetic acid. The acetic acid evaporates and leaves the glycerine; this tends to plasmolyse the cells so that the cytoplasm shrinks, but the chromosomes are still visible. The method was originally used with aceto-carmine, and works reasonably well with it; the results with orcein were less satisfactory. This method has the advantage of lasting longer than a preparation which has been merely sealed (although it was found desirable to seal these mounts too), but they cannot be considered really permanent.

Various stain-fixing-mounting media were also tried out (Traub, 1950, 1953; Zirkle, 1940), but they were found to be unsatisfactory, usually because the liquid was too viscous to allow sufficient maceration of the material. In general, the simplest, quickest technique was found to be the best, provided that the slides were examined within a few days.

A few of the really good slides were made permanent (usually after a count had been obtained from them). The cover-slip was soaked off in 45% acetic acid; the slide and cover-slip were then transferred to 70% alcohol, and two changes of absolute alcohol; they were then mounted separately in Euparal. This certainly gives the best preparation, but for large numbers of slides it is slow, and there is always the risk of losing the few really good cells on the slide.

The use of semi-permanent preparations means, of course, that much of the evidence is lost; this can be remedied by photographing every preparation as it is made. When only the chromosome number is required, this seems rather unnecessary, and it was found to be impractical, mainly on financial grounds, but also because of the time required to develop large numbers of plates.

Photography.

Despite the impracticability of photographing every slide as it was made, photographs were obtained of representative slides of the different taxa counted, and these are illustrated in plates 17 - 24.

The photographs were taken on $3\frac{1}{4} \times 2\frac{1}{4}$ inch plates in a Baker microscope camera attachment. The light was equipped with a green filter to give the maximum contrast. Different types of plate were used, but a completely satisfactory one was not found. The amount of contrast on the plate was never sufficient, and they were all printed on Kodak Extra Hard paper. The original preparations were probably not deeply enough stained to show up well in the photographs, and the light may not have been adjusted correctly.

B. RESULTS.

The material used was from two sources:- 1) seed from the wild populations, and 2) the plants grown in the experimental garden.

The results for the first group are summarised in table 12, and those of the second group in table 13. Photographs from a few of the slides are included among the plates.

The first group of results can be related to the population studies described in the last chapter. This relationship must be treated with caution, since the plants whose chromosome numbers were counted were the progeny of the plants whose morphology was studied. The method used for making the preparations was that described in A 2. above, using seedlings.

The second group of results, from plants grown in the experimental garden can be related to the morphological characteristics of the plants themselves, and are therefore more valuable to the taxonomist than are those in table 12. The technique used was described in A 3 above, using ovary walls.

1). <u>Chromosome Counts from Wild Populations</u>.

The results are summarised in table 12; they are all from diploid material. Counts were obtained only from those populations collected in the first two years of the investigation, that is, from populations I to XVII. Varying numbers of plants from each gathering were counted; the more variable the parent population was, the larger the number of seedlings from which a count was obtained. The technique being far from perfect, a number of doubtful counts were obtained; these have been included in a separate column in table 12, and a third column gives the total number of counts, "good" and "doubtful" which were obtained.

TABLE 12

CHROMOSOME NUMBERS DETERMINED FROM SEEDLINGS

Population	2n	Number of plants counted good	doubtful	total
I A	12	8		8
I B	12	1		1
	30	~~1~~	1	1
	36	1	1	2
	42		2	2
	48	1		1
				7
I C	12	1		1
	42		1	1
	48	2	2	4
				6
II A	36	1		1
II B	48		2	2
II C	12	2		2
II F (i)	36		1	1
	42	1		1
	48	2		2
				5
II F (ii)	42	1		1
	48	5		5
				6
II F (iii)a	12	2		2
	42	1		1
	48	3	2	5
				8

TABLE 12 continued.

Population	2n	Number of plants counted		
		good	doubtful	total
II F (iii)b	12	6		6
	42	1		1
	48	6	1	7
				14
II F (iv)	12	9		9
III A	36	1		1
III C	36	1	1	2
	48	1		1
				3
III D	42		1	1
	48		1	1
				2
IV A	42		1	1
	48	1	1	2
				3
IV B	42	1		1
	48	5	~~5~~	5
				6
IV C	42	1		1
	48	3	2	5
				6
V A	48	1	1	2
V B	36	1	1	2
	42		3	3
	48	3		3
				8

TABLE 12 continued.

Population	2n	Number of plants counted good	doubtful	total
V C	30		1	1
	36	3	2	5
	48	1		1
				7
V D	36		2	2
	42		3	3
	48	1	1	2
				7
VI	30		1	1
	36	3		3
				4
VII A	48	3	1	4
VII B	36	2		2
	42		1	1
	48	2	1	3
				6
XII A	48	1	1	2
XII B	12	1		1
XIII A	48	1		1
XIII B	48	2		2
XIII C	48	1		1
XIV A	42		1	1
XIV B	48	1		1
XIV C	42		1	1
XIV D	48	1		1

TABLE 12 continued.

Population	2n	Number of plants counted		
		good	doubtful?	total
XV	36		1	1
	48	1		1
				2
XVI	48	1		1
XVII	12	1		1
	48	1		1
				2

These results are probably best related to the proportions of the different taxa found in each population, shown in table 9, and to the ogives of X, Y and Z for the different populations. It must, of course, be borne in mind that the results are what might have been obtained from a future generation of plants. It is possible that those with intermediate numbers (2n = 30, 42) would not in fact survive to grow into adult plants. However, they may throw some light on the breeding systems existing in wild populations.

I A. Eight counts were obtained, all of 2n = 12. The population analysis gives over 80% of the plants as campestris, so that a larger sample would probably have been required if the other taxa were to be included in the counts.

I B. A total of seven counts was obtained, four of which were doubtful. The three good counts are for 2n = 12, 36 and 48, which seems reasonable, as the population contains campestris, multiflora and congesta. There is a doubtful count of 2n = 36, one of 2n = 30, and two of 42. The first of these is quite probably correct; the second might be the result of a cross between congesta (48) and campestris (12), although there seemed no indication of such hybrids in the population analysis; the third could be a cross between multiflora (36) and congesta (48), a hybrid which seems to be of relatively frequent occurrence.

I C. There were six counts, three good and three doubtful; two of the good counts were of 48, and one of 12, corresponding to the congesta and campestris in the population. The doubtful counts were two of 48 and one of 42. The sample should obviously have been larger, when it might have included some hexaploid multiflora, which makes up a significant proportion of the group.

II A. Only one count was obtained, of 2n = 36; this population is mostly multiflora, but there were some plants of congesta, so that a larger sample would probably have contained some octoploids.

II B. Only two doubtful counts were obtained, both of 2n = 48; since the population was over 70% congesta these are probably correct.

II C. Two counts of 2n = 12; over 80% of the plants were campestris

II D. No counts.

II F.(i) One doubtful count of 36 was obtained; there are no plants of multiflora in the population, so it is probable that this is wrong. One count of 2n = 42 could correspond to the 5% of intermediate forms in the population, while the two octoploids represent the congesta which makes up over 90% of the population.

II F.(ii) The five counts of 2n = 48 correspond to congesta, of which this population was entirely composed. The single count of 42 is probably the result of one of these plants crossing with a hexaploid plant from another population.

II F (iii)a. This population contained _campestris_ and _congesta_, with one or two plants of _multiflora_. The chromosome numbers are of two diploids (_campestris_); four octoploids, two of them doubtful (_congesta_); one plant with 2n = 42, possibly from _congesta_ or _multiflora_ as the result of crossing.

II F (iii)b. This population also was mixed, but it had over 50% _campestris_, compared with only 20% in (iii)a. This is reflected in the presence of six counts each of 2n = 12 and 2n = 48. One plant with 2n = 42 was also found, and possibly resulted from crossing as before.

II F (iv). All the plants measured were _campestris_, and all the nine seedlings counted were diploids.

III A. There was only one count obtained, 2n = 36; nearly 90% of the plants were _multiflora_, so that far more seedlings would have had to be counted before any octoploids were found.

III B. No count.

III C. There were two hexaploids, one good and one doubtful, and also one octoploid. The origin of the latter is a problem, since there were neither true _congesta_ nor intermediate forms in the population, which was over 80% _multiflora_, with some _campestris_.

III D. Only two doubtful counts were obtained, one of 42 and one of 48. The population is nearly 70% <u>congesta</u>, with a few plants of <u>multiflora</u> and a few intermediates.

IV A. This population was nearly 70% <u>congesta</u>, and there was one good count of 48, and one doubtful. There was also a doubtful count of 42, which is quite possible, since there is also a proportion of <u>multiflora</u> and of intermediate forms.

IV B. This population also had about 70% <u>congesta</u>, reflected in the presence of five octoploids; the one plant with $2n = 42$ is probably due to the existence of some plants of <u>multiflora</u> in the gathering.

IV C. Over 70% of this population was <u>congesta</u>, and three good and two doubtful octoploids were found. The presence of some plants of <u>multiflora</u> account for the one count of $2n = 42$

V A. This gathering had over 60% <u>multiflora</u>, but the only count from it was an octoploid. It is obvious that more counts should have been made.

V B. The population was about 80% <u>congesta</u>, and there are three counts of $2n = 48$ which correspond to this taxon. There are also one good and one doubtful hexaploid, and three doubtful counts of $2n = 42$, all of which are due to the presence of a few <u>multiflora</u> plants in the population.

V C. The population was made up of over 50% <u>multiflora</u> and about 30% <u>congesta</u>, with a few intermediates. The chromosome counts gave five hexaploids, two of them doubtful, and one octoploid. There was also one doubtful count of $2n = 30$, which is probably an error, but might just possibly be a cross between campestris and congesta.

V D. There was mostly multiflora in this population, with a few plants of congesta and no intermediates. The counts gave two doubtful hexaploids (multiflora), one good and one doubtful octoploid (congesta), and three doubtful counts of $2n = 42$, which, if correct, must have come from either multiflora or congesta plants, and must be the result of these two having crossed.

VI. Over 80% of the population was multiflora, and there are three hexaploids counted from it. There is also one doubtful count of 30, whose origin is uncertain, but it is probably incorrect.

VII A. The population was made up of over 60% of congesta; four octoploid plants were counted, one of them doubtful.

VII B. This population was a mixture of multiflora and congesta and had a high proportion of intermediates; there was a considerable number of plants which were partially sterile. Two hexaploids, and two octoploids were found, with a further doubtful octoploid. There was also a doubtful count of $2n = 42$; more plants in this category might have been expected, but partial sterility of the intermediate plants might account for this, and also the small size of the sample.

The next group of populations has been even less adequately treated, only one or two plants from each having been counted.

XII A and B. The former was over 80% congesta, and one octoploid was counted; the latter is campestris, and the only count is of 2n = 12.

XIII A, B and C. All the populations were predominantly congesta, the proportions being 60%, 50% and 90% respectively. All the plants counted were octoploids, one each from A and C, and two from B.

XIV A, B, C and D. The first three were predominantly multiflora, the last congesta, with 50%, 60%, 60% and 30% multiflora respectively. One octoploid was counted from B and C, and one plant with 2n = 42 from A and D.

XV. This population was most congesta, with a few multiflora, and the counts have one octoploid and one doubtful hexaploid.

XVI. There were about 60% multiflora and 30% congesta, but the only count was of one octoploid.

XVII. The population was mostly congesta, with some multiflora and some campestris; one diploid and one octoploid were counted.

This last group of populations has so few counts from it, that it seems inadvisable to include them in the discussion of the relation of chromosome numbers to the structure of the population.

It is obvious from these results that the number of chromosome numbers counted is seriously inadequate for the proper consideration of the relationship of the relative proportions of the taxa present in a population and of the different chromosome numbers obtained from their progeny. For a really valid comparison to have been made it would have been necessary to have counted a much larger sample of seedlings from each population, preferably the same number as there were plants originally, or at least 20 in every case. The preparation of slides, and their subsequent examination is a time consuming process, and about two thirds of the slides made had no metaphase plates, and not all of those which did were good enough to give a chromosome count. Possibly it would have been better to have examined a large sample from only one or two of the mixed gatherings, or groups of gatherings (e.g. VII B, II F (i)-(iv), and to have done the other populations even less adequately. Another possibility is to add together the percentages of the various taxa occurring in the populations I A to VII B, and also to add the number of times each chromosome number occurs in these populations. This effectively combines all the plants into one large gathering; they are all in fact from the same area, around Loch Tay.

The results are summarised below:-

Name	Number of Plants		2n	Number of Counts
	a	b		
campestris	365	364	12	29
multiflora	1060	885	36	21 = 13 + (8)
congesta	1072	1086	48	55 = 40 + (15)
campestris x multiflora	14	30	-	0
campestris x congesta	0	19	30	(3)
congesta x multiflora	89	199	42	18 = 6 + (12)
campestris/ congesta/ multiflora	0	26	-	0

The two columns of numbers following the names of the taxa are the sums of the percentages present according to a) the straightforward index, and b) according to the modified index, as in table 9. The numbers in brackets in the last column are the doubtful counts.

These results are obviously not very well correlated, but this can be explained in various ways. The number of diploid plants is a much higher proportion than the number of campestris plants determined morphologically. This is undoubtedly due to the fact that it is much easier to count 12 chromosomes than it is to count 36 or 48. This meant that a far higher proportion of the slides made of campestris contained a cell whose chromosomes could be counted. The number of hexaploids is much lower than would have been expected from the proportion of multiflora in the analysis. This is probably because only a few plants were counted from each of the populations where multiflora is predominant, e.g. II A, IIIA, B, C, etc. The relative proportions of the intermediate plants and congesta suggest that the total number of counts of 42 (18) is high compared with the number of octoploids (55); the proportions of congesta to intermediate are a) 1072 : 89 = approx. 12, and b) 1086 : 199 = approx. 5.5. The number of octoploids is only three times the number of hybrid numbers, but could have been expected to be nearer five times. If the doubtful counts are ignored, as perhaps they should be, then there are more than six times the number of counts of 48 as there are of 42. The high proportion of 2n = 42 could be because more seed is set with this number, but the seedlings are at a disadvantage in the natural environment, and do not all reach maturity. The high proportion of doubtful counts in this group, 12 compared with 6 good counts, indicates that perhaps the total may be higher than it should be, and that the comparison of only the good counts is more reliable, and this compares quite closely with the proportions of congesta and the intermediate forms in the unadjusted index. This supports the view that this index gives a better indication of the structure of the populations than the modified interpretation of it, and that the intermediate forms very probably are indeed hybrids.

The results from these wild populations are inconclusive, but they do show that the chromosome numbers found correspond generally to the proportions of the different taxa occurring in each gathering. The amount of work carried out in this respect is insufficient to do more than add a little weight to the conclusions already drawn, namely that while intermediate forms between multiflora and congesta are relatively frequent (2n = 42), intermediates between campestris and the other taxa are rare. The only possible hybrids between campestris and the other taxa are the three doubtful counts of 2n = 30 obtained from IB, VC, and VI. The result of a cross between the diploid campestris (2n = 12) and the octoploid congesta (2n = 48) would be a plant with 2n = 30; since these results are in any case doubtful, very little significance can be attached to them.

The counts of 2n = 42 probably do correspond to what would have been intermediate plants between multiflora (2n = 36) and congesta (2n = 48); they may have come from seed produced by either of the taxa in the original population, as the result of fertilisation by the other,

TABLE 13.

CHROMOSOME NUMBERS OF PLANTS GROWN IN CULTIVATION

	2n		2n
Davis 20/4	12	Davis 18/2	42
Davis 21/4	12	Davis 23/1	42
" " 5	12	2	42
Davis 22/2	12	3	?48
		4	48
Buchanan 2b/1	36	Davis 37/1	48
2	36	2	?42
3	36	3	?42
4	36		
5	?36		
		migrata	16
Henderson 18/2	36	pallescens	12
3	36	forsteri	24
4	36	sylvatica	12
5	36	pilosa	c.60
Henderson 17/1	?36		
2	36		
3	36		
4	36		
5	36		
Davis 68/1	48		
5	48		
Buchanan 1b/2	48		
5	48		

or from already existing intermediate forms. The evidence from the cytology lends support to the opinion that many, if not all, of the forms found to be intermediate between multiflora and congesta, on morphological analysis, are probably of hybrid origin.

2) Chromosome Counts from Cultivated Plants.

The plants grown in the experimental garden were collected by different people in different parts of the country. About 5 or 6 plants were grown from each gathering, and there were three gatherings each of campestris, multiflora and congesta, and three of mixed multiflora and congesta. The plants were collected and measured, and the morpholofical characters analysed, as described in the previous chapter.

Chromosome counts for as many of the plants as possible were obtained, particular attention being paid to multiflora and congesta, so that rather fewer of the campestris plants were counted. The results are shown in table 13.

The populations of campestris are Davis 20, 21 and 22; those of multiflora are Buchanan 2b and Henderson 17 and 18; congesta are Davis 68, and Buchanan 1 and 1b; the mixed populations are Davis 18, 23 and 37. No counts at all were obtained for Buchanan 1; the herbarium specimens were collected in the summer of 1955, and the counts were made during the following two years, but by that time this particular gathering had died out.

The results show that all the plants counted from the campestris gatherings were diploids ($2n = 12$), which is what would be expected as none of the plants appeared to be anything other than pure campestris.

The counts from the congesta populations are all of $2n = 48$, which would again be expected, as they were all typical congesta. More counts of the multiflora plants were obtained than for any of the other groups, and they were all hexaploids with $2n = 36$. These two groups of gatherings seem therefore to be more or less pure.

The third group of populations shows more morphological and cytological variability, but counts were unfortunely not obtained from all the plants in them. Each gathering has, however, at least one plant with $2n = 42$, and two of them have octoploids as well.

Table 14 shows the X and Y indices of these plants, together with the corresponding chromosome numbers. There appears to be a considerable lack of correlation between them, some of the "multiflora" types (with lax inflorescences) have chromosome numbers of 42, and one is even an octoploid (Davis 37/1). The other octoploids have Y = 88 and 89 (Davis 68/1 and /5), and are more typically congesta. No hexaploids were found in these gatherings, although, of course, had all the plants been counted some might have been found.

A scatter diagram of X and Y was drawn, and different symbols were used to represent the different chromosome numbers (fig. 104). This diagram shows that the relationship of chromosome number to the morphology is rather closer than appeared from the comparison of the results in tabular form.

The plants show three clearly separated groups. In the campestris group four plants were counted, all of them diploids, and there is no reason to think that any of the other plants would have a number other than 2n = 12. The other two groups are separated by the Y index, and there is a gap between Y = 75 and Y = 85; this is shown also in the histogram of Y for multiflora, congesta and the mixed gatherings combined, fig. 105. Here there is a small gap between 64 and 68, then a group of four plants with Y = 69 - 75, followed by a larger gap between Y = 76 and Y = 85. This scatter diagram shows that all the hexaploids (2n = 36) have a value of Y less than 65, and that this group is composed of true multiflora. This group also has one plant with 2n = 42 (D 37/2), which has a value of Y = 52. The other large group contains all the octoploids except one, which has a value of Y = 75; the remainder are all over 85. The congesta group also contains one plant (D 23/2) with 2n = 42, which has Y = 102. The small group of four plants with Y = 68 - 75 includes the octoploid mentioned above (D 37/1) and three septaploids with Y = 69, 69 and 71 (D 37/3, D 23/1 and D 18/2) respectively, one from each of the mixed populations.

The diagram shows that while one octoploid plant did at first appear to be multiflora, it is situated at the extreme edge of this group, and is separated from it by three septaploid plants. This octoploid was from one of the mixed populations; all the octoploids from the pure congesta populations have Y greater than 90. The distribution of the five plants with 2n = 42 shows that three of them are more or less intermediate morphologically, although approaching multiflora rather than congesta, while there is one plant in each of the multiflora and congesta groups.

The evidence from this part of the investigation helps to support the use of an index made up of three diagnostic characters, rather than relying on the best of these characters (the degree of congestion of the inflorescence) alone, to separate multiflora and congesta. The octoploid with a low value of Y had a lax inflorescence, but the perianth segments were abnormally large for multiflora, and this helped to increase the index so that the plant was in a more intermediate position. It is not certain whether this plant is pure congesta; either the octoploid number of chromosomes is not perfectly correlated with the congested inflorescence, or this plant is the result of a multiflora x congesta hybrid back-crossing with congesta, so that the octoploid number has somehow been regained. The three intermediate septaploids had also all lax inflorescences, but, again, the seeds and perianth segments were relatively large. The only septaploid with a congested inflorescence is in the congesta group.

This suggests that the lax inflorescence may be dominant over the congested, since four out of five presumably hybrid forms have lax inflorescences. It would be desirable to substantiate this theory by carrying out artificial crossing experiments, and then raising the progeny.

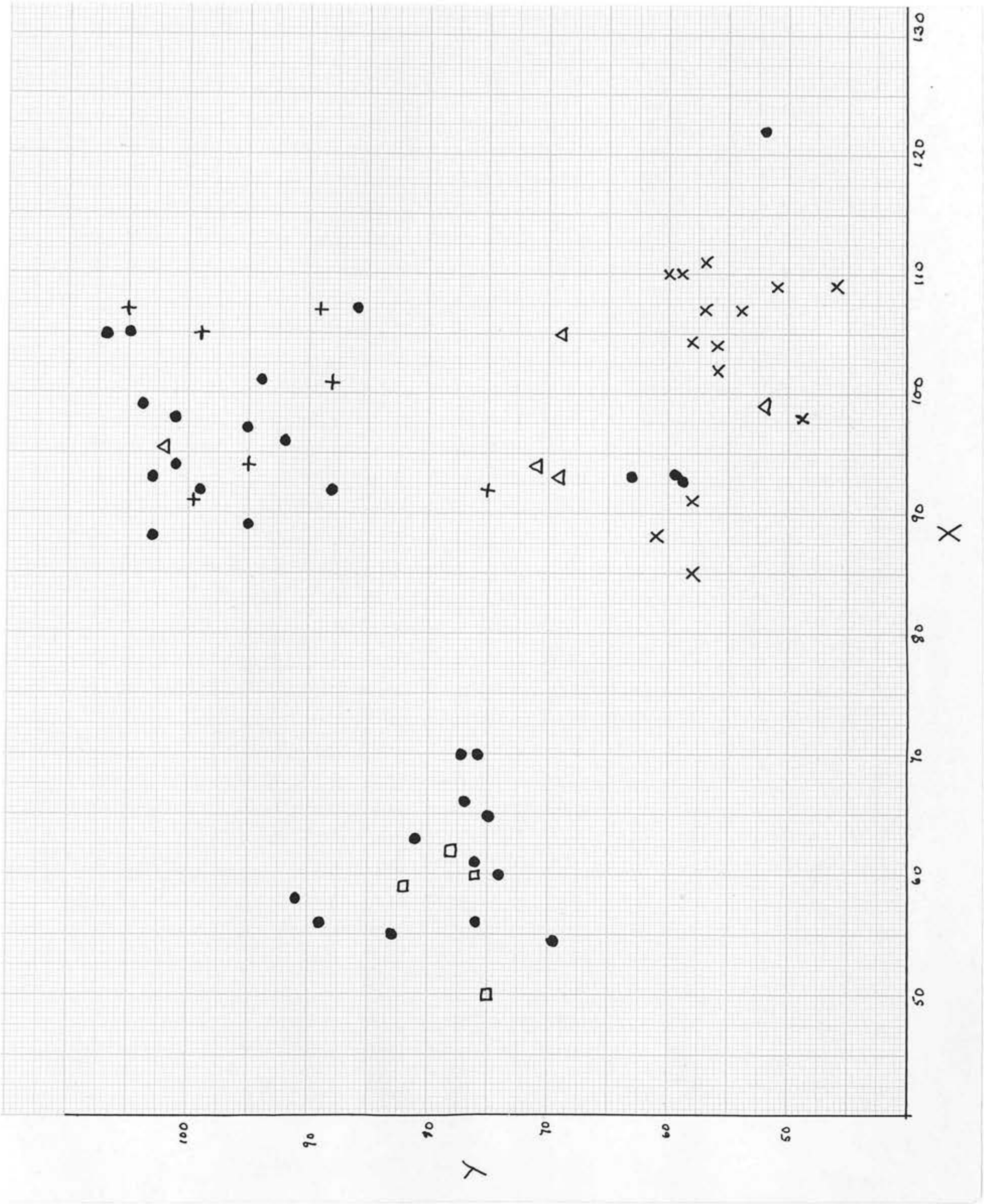


Fig. 104. Scatter diagram of X and Y of the cultivated plants, with chromosome numbers.

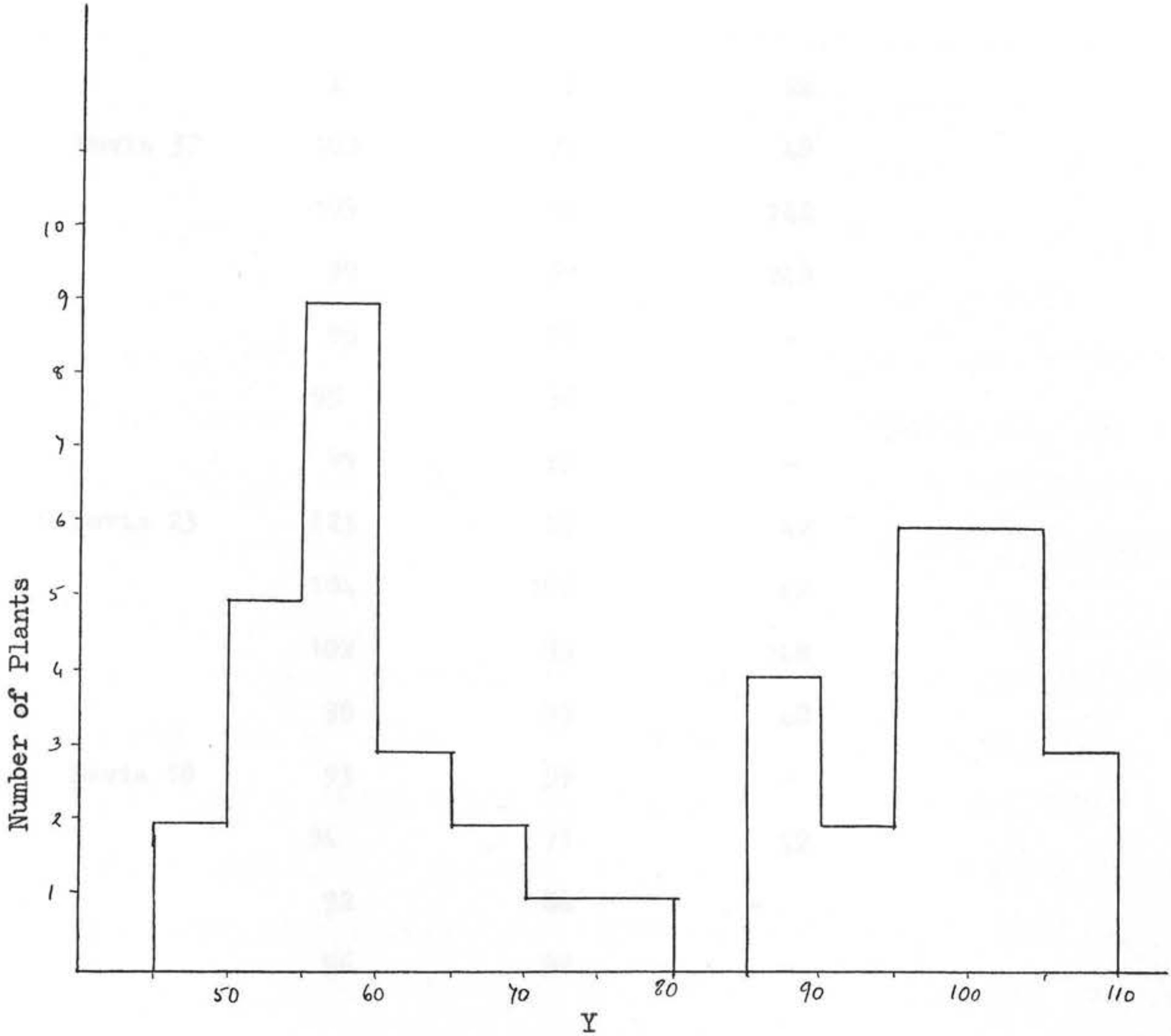


Fig. 105. Frequency histogram of Y for the cultivated plants of multiflora and congesta.

TABLE 14.

CHROMOSOME NUMBERS AND X AND Y INDICES OF THE MIXED GATHERINGS OF CULTIVATED PLANTS.

	X	Y	2n
Davis 37	100	75	48
	109	52	?42
	99	69	?42
	95	59	-
	95	95	-
	99	63	-
Davis 23	123	69	42
	104	102	42
	102	95	?48
	98	99	48
Davis 18	93	59	-
	94	71	42
	92	88	-
	96	92	-

C. CONCLUSION.

The results obtained in this study correspond fairly closely with those of Nordenskiold and other workers. In one respect, however, the interpretation has been made easier, since only one of the chromosome races of multiflora and of congesta were found in the British material used. Nordenskiold found tetraploid (2n = 24) and hexaploid (2n = 36) multiflora, and hexaploid and octoploid (2n = 48) congesta. Neither the tetraploid multiflora nor the hexaploid congesta were found in any of the material examined. Apparently the only character used by other workers to distinguish congesta from multiflora is the congestion of the inflorescence. Careful correlation of the chromosome number with the morphology seems to indicate that this character, while usually reliable especially in pure populations, may break down when crosses, and possibly also backcrosses, are obtained. The octoploid plant with Y = 75 would presumably be considered by many people to represent an actoploid race of multiflora; in fact, this plant seems not to be pure multiflora or congesta, but is morphologically nearer to the hybrid plants (2n = 42). It is possible that this plant might be a backcross between an octoploid congesta and a septaploid hybrid which has been restored to the octoploid chromosome number, and has become stable. If the lax inflorescence is in fact dominant over the congested, it could account for the fact that this plant, and four of the five septaploids, have lax inflorescences.

The Luzula campestris complex is not the only case where related taxa have lax and congested inflorescences in the Juncaceae. Several other cases exist in Luzula, e.g. L.comosa E. Mey. var. congesta Watson and var. laxa Buchenau; L.spicata (L) DC s.s. and var. laxa Hoppe. In Juncus there are numerous other examples: J.effusus L. and J.conglomeratus; J.compressus and its variety coarctatus; J.acutus L. var. effusus Buchenau and var. conglomeratus Buchenau. (These examples are all taken from Buchenau's Monograph). The nature of the congested inflorescence in the Juncaceae as a whole would possibly be a rewarding study: the difference between the lax and congested forms may be caused by a single gene, or it may be, as suggested by Anderson + Stebbins (1954), that congested inflorescences are correlated with higher degrees of polyploidy. If the first case is true, then the same gene must affect both seed size and perianth size as well; the correlation of these characters does not seem to be sufficiently high to uphold this theory. The second case may be possible, since congesta does have a higher degree of polyploidy than multiflora, but comparable studies in far more pairs of taxa would be required before this theory could be substantiated.

The results obtained from plants grown under cultivated conditions and from those from seedlings from the wild plants correspond fairly well with what might have been expected from the analysis of the morphological characters. The population studies indicated that campestris was less closely linked to multiflora and congesta than these two are to each other, and that intermediate forms between the two latter are more common than between either of them and campestris. If this is a correct observation, then it might be expected that the cytological investigation would show the existence of more hybrids between congesta and multiflora than between either of them and campestris; this is what is, in fact, found.

The hybrids between campestris and multiflora would have 2n = 24 (n = 6 + n = 18); between campestris and congesta the number would be 30, and between congesta and multiflora, 42.

The number 2n = 42 occurs quite frequently; in the wild populations it is found where multiflora and congesta are mixed, although there may have been no intermediates in the parent population. In the cultivated plants the septaploids again occur where lax and congested forms have been collected from the same population; here they are correlated with intermediate values of the Y index. It seems reasonable to assume that these plants with 2n = 42 are indeed hybrids between congesta and multiflora, although they are not always exactly intermediate morphologically.

No plants with 2n = 24 were counted, although the population analyses indicated that some interbreeding of campestris and multiflora might have been possible. There were three doubtful counts of 2n = 30; these might have been crosses of campestris with congesta, but as they are doubtful, it seems best to treat them as errors.

In conclusion, the cytological evidence confirms the view derived from the study of the morphology and ecology that there are three distinct taxa in this group of plants common in Britain, and that, although they may grow close to each other in the field, they do manage to retain their separate identities. Hybrids between multiflora and congesta are quite frequent where these taxa grow together; hybrids between either of these and campestris are rare.

D. OTHER CHROMOSOME COUNTS.

The other British species of Luzula were grown in the experimental garden; L.arcuata did not survive, and L.spicata did not grow very well, so that no counts were made for either of them. Counts were, however, made for L.sylvatica (2n = 12) and L.forsteri (2n = 24). Preparations from L.pilosa were not very satisfactory, since the chromosomes are small and so numerous; the number counted was 2n = c.60. These counts are all in agreement with the numbers obtained by other workers.

Two additional members of the campestris complex were grown: pallescens, from Woodwalton Fen, and migrata from Australia. The count of 2n = 12 for pallescens is the same as that obtained by other workers.

The count for migrata was 2n = 16. This plant is interesting, as it shows Nordenskiold's "endo-nuclear" polyploidy. The set of chromosomes is made up of eight large and eight small ones (see plate 24). The eight small chromosomes have presumably been derived by the transverse splitting of four large ones; the original type was probably a diploid with twelve large chromosomes.

VII. DISCUSSION AND TAXONOMIC CONCLUSIONS.

The previous chapters contain the evidence on which the taxonomic conclusions must be based; this evidence comes from four main sources:-

Morphology

Geographical distribution

Ecological distribution

Cytology

The examination of herbarium specimens shows that the group of plants described by Buchenau (1906) as Luzula campestris (L.) DC: is morphologically very diverse, and geographically very widely distributed; indeed it is almost cosmopolitan.

By plotting the geographical distribution of the individual morphological units, it is found that no two of them cover exactly the same area; differences in morphology are correlated with differences in geographical distribution. The morphological units (varieties in Buchenau's Monograph) are not completely distinct from each other, and a small proportion of the herbarium specimens is impossible to fit into any of the categories. The areas occupied by these units also overlap, so that any part of the area covered by the whole complex may contain up to six of the smaller units. The presence of these unidentifiable "intermediate" forms, and the degree of overlap of the areas occupied by the different taxa, led Buchenau to consider all these different morphological types as varieties of the one species, L.campestris.

Not all authors and writers of Floras have followed Buchenau; the rank assigned to the taxa ranges from variety to species. To add to the confusion, different authors have assigned specific rank to different taxa, and have made an assortment of other taxa varieties or subspecies of these. Very few of the Floras consulted gave exactly the same classification as any of the others, and remarkably few followed Buchenau. This is unfortunate, for, while some of the taxa undeniably deserve more than varietal rank, he did consider the group as a whole in its distribution throughout the world. Other authors have tended to look only at their own small areas, and to ignore the rest of the world.

The present study has attempted to survey the whole of the group in its world-wide distribution and to examine in as much detail as possible the relationships of the three taxa which occur commonly in a very limited area of the world, the British Isles.

When more than one taxon is found in any given area (Europe, North America, Australasia, Japan, etc.) examination of the herbarium labels (if adequate) and of the literature will reveal that these taxa often frequent different habitats. For example, of the six taxa found in Europe, campestris grows in dry grassy places, pallescens in woods and damp open places, congesta in moors and bogs, multiflora in woods and damp meadows, sudetica in mountainous and alpine regions and frigida in the arctic region, but also in the mountains farther south. In New Zealand, picta grows in woods and australasica and crinita in the mountains; migrata is more widely distributed.

A source of information which was not available to Buchenau is the cytology of the group. Had this been available at the beginning of the century, he would probably not have lumped all the taxa together into one species. The chromosome numbers of various members of the complex have been counted, and are summarised in table 11. Had the same number been recorded for all of them, and had they all been completely inter-fertile, then there would have been no reason to alter Buchenau's classification; all the taxa described by Buchenau, and any described since, would have had to be recognised as subspecies of campestris. Unfortunately for the simplification of the literature and the nomenclature, this is not the case. The plants have been shown to fall into a polyploid series, with numbers ranging from 2n = 12 to 2n = 48. This is further complicated by the phenomenon of "endo-nuclear" polyploidy, so that some taxa have a large number of very small chromosomes, but most be considered at the diploid level because the amount of chromatic material in their nuclei is equivalent to that found in normal diploids with 2n = 12 (e.g. sudetica has 48 small chromosomes). The different chromosome numbers are correlated with the morphological units, and with their geographical distribution. The occurrence of hybrids, natural and artificial, between different taxa indicates that their affinities are probably quite close. While some species in the group may be of relatively recent origin, and are probably still in a state of active evolution, the group as a whole may be much older.

The detailed examination of the three taxa commonly found in Britain (_campestris_, _multiflora_ and _congesta_) showed that they are morphologically quite well separated from each other. _Campestris_ is a much smaller plant than _multiflora_ or _congesta_, and in addition, it differs from them in five floral characters. _Multiflora_ and _congesta_ are very similar vegetatively, but they can be distinguished by three floral characters.

The habitat differences are not absolute, those of any two, or of all three taxa may converge on each other, and _multiflora_ and _congesta_ in particular show considerable tolerance of each other's habitat. The ecological separation may not be sufficient to prevent hybridisation completely in the case of _multiflora_ and _congesta_, but it indicates at the very least a physiological difference between the taxa, which might be interpreted as a further taxonomic character. There is also a marked difference in flowering time between _campestris_ and the other taxa, but little difference between _multiflora_ and _congesta_.

The correlation of cytological, ecological and morphological differences between _multiflora_ and _congesta_ seems to be strong enough to outweigh the presence of hybrids between these taxa, and to warrant specific rank for them; the name _L.campestris_ would be restricted to the former variety of that name.

If these three taxa can be given specific rank, then it seems to be logical to extend this rank to all the taxa in the complex which, on examination of the herbarium material, and on reference to the geographical distribution and to the chromosome number (if known), show differences between them of equal or greater magnitude than those distinguishing multiflora from congesta. Specific rank is accordingly proposed for the following varieties of L.campestris (L.) DC. as described in Buchenau. The varietal name given in the Monograph is followed by the corresponding specific name and the authority.

Variety.	Species.
vulgaris Gaud.	L. campestris (L.) DC.
Mannii Buchenau	L. mannii (Buchenau) Buchanan
picta (Less.& Rich.) Hook.f.	L. picta Less.& Rich.
pallescens Wahlenb.	L. pallescens (Wahl.) Bess.
pauciflora Buchenau	L. oligantha Sam.
sudetica (Willd.) Čelak.	L. sudetica (Willd.) DC.
tristachya (Desv.) Buchenau	L. tristachya Desv.
Banksiana (E.Mey.) Buchenau	L. banksiana E. Mey.
congesta (Thuill) Buchenau	L. congesta (Thuill.) Lej.
australasica (Steud.)Buchenau	L. australasica Steudel
capitata Miquel	L. capitata (Miq.) Nakai
Petrieana Buchenau	L. petrieana (Buchenau) Buchanan
floribunda Buchenau	L. floribunda (Buchenau) Buchanan
crinita (Hook.f.) Buchenau	L. crinita Hook. f.
frigida Buchenau	L. frigida (Buchenau) Sam.
migrata Buchenau	L. migrata (Buchenau) Ostenfeld
multiflora Čelak.	L. multiflora (Retz.) Lej.

Three new combinations are proposed in the above list :-

Luzula mannii (Buchenau) Buchanan

L. petrieana (Buchenau) Buchanan

L. floribunda (Buchenau) Buchanan

The following should also be considered as species :-

L. bulbosa (Wood) Rydb.

L. echinata (Small) F.J. Hermann

The following should perhaps be considered as species, but their rank is less certain:-

L. cusickii Gandoger. This is from a very limited area in North West America. Most of the specimens seen are from the same gathering (Cusick 2248) as the type. It is difficult to assign it to any of the other taxa; it was collected by Cusick under the name L. campestris, but it is obviously not this species. There appears to be some affinity with L. racemosa Desv. (Gandoger, 1920).

L. kjellmanniana Miyabe & Kudo. This is described by Samuelson as a variety of multiflora (L. multiflora var. kjellmanniana Sam.); it was also described as a variety of L. arcuata (L. arcuata var. latifolia Kjell.); it is probably also synonymous with L. confusa var. latifolia Buch. (Miyabe and Kudo, 1913).

L. kobaysii Satake. This seems to be morphologically between L. frigida and L. comosa var. laxa. (Satake, 1932).

The rank to be given to the following is doubtful:-

calabra (Ten.) Buchenau. No specimens were seen; the plant is very local and differs from the rest of the group in having a spicate inflorescence. Buchenau describes it as resempling L. comosa var. macrantha Watson. It should possibly be L. calabra Tenore.

flaccida Buchenau. Plants approximating to this taxon were examined in the herbaria, most of them from Tasmania. The plants are very small and have few flowers; they appeared to be reasonably distinct, but it is possible that they are only a shade form.

debilis Velenovsky. This seems to be an eastern European and Central Asian form close to L. sudetica, but with larger perianth segments and seeds; it may be intermediate between that species and multiflora.

acadiensis Fernald. This plant is from eastern Canada; it is described as a variety of multiflora, but is not very well distinguished from it, although it is smaller.

In all these four cases the number of specimens available was very small, and not all identifications were certain. More abundant material might make it possible to come to a definite decision regarding their rank.

While the evidence justifies giving specific rank to most of Buchenau's varieties, it must be recognised that they do form a natural group of species, closely related to each other, and to other species of Luzula not included by Buchenau under campestris (particularly L. comosa and L. racemosa). The group forms a polyploid series, the individual members of which are morphologically distinct, and geographically or ecologically separated. It might be possible to regard the group as a whole as a supra-species and most of the individual members as ecospecies; in this case it might be possible to regard some of the doubtful taxa as ecotypes, but without adequate experimental evidence this would be unwise.

The application of the "deme-terminology" (Gilmour and Heslop-Harrison, 1954) to these plants might provide a basis for demonstrating the differences between the species, and at the same time showing up their affinities with each other. In this case the individual taxa would be "eco-cyto-demes", etc.

While the deme terminology might allow the relationships within the group to be illustrated, it has not yet been generally accepted by botanists, and it does little to clarify the status of the plants in the orthodox taxonomic system. It appears that the best method is to recognise the individual units as separate species, since they are morphologically, cytologically and geographically different. The correlation of differences of chromosome number with even small morphological differences, is considered by Valentine and Löve (1958) to justify specific rank. To give specific rank to the majority of the morphological units in this group of Luzula does not set a precedent; species have been separated from each other in other genera of flowering plants on what seems to be much less substantial evidence, and while this is not in itself a valid reason for raising still other plants to specific rank, it indicates that such a decision falls in line with those of other botanists working along similar lines with other genera. Although all the chromosome numbers have not yet been determined, it would seem illogical to give specific rank only to those whose chromosome number is known, and not to the remaining taxa.

To give specific rank to all of the taxa may obscure the affinities between them, but if they are regarded as a species complex, or as an aggregate species made up of a polyploid series, then the affinities will be given equal emphasis with the differences which justify specific rank.

The origin of the polyploid complex is uncertain. The diploid species are ~~the~~ very different morphologically, and represent in many ways the extremes of variation, especially campestris and pallescens. The former has very large, dark coloured flowers, while the latter has a much larger number of exceedingly small, light coloured flowers; it would be impossible ever to confuse the two. Nordenskiold (1951) believes the tetraploid multiflora to be an autotetraploid of pallescens, and that the hexaploid race is the result of a back-cross of this tetraploid with pallescens.

L. sudetica, although it has 48 chromosomes, is, because of endo-nuclear polyploidy, also at the diploid level; it has very small dark flowers. L. frigida is in some ways intermediate between multiflora and sudetica. L. congesta has very large perianth segments, and might possibly be the result of introgression of campestris into a multiflora stock, with the congested inflorescence resulting from subsequent polyploidy.

Buchenau considered multiflora to be the ancestral form of the complex, because of its very wide distribution in the northern hemisphere. Since this species is either a tetraploid or a hexaploid, this now seems unlikely, and it appears to be most probable that the species complex has arisen by the interaction and hybridisation of the original diploid species (which must have arisen from the same stock), along with autopolyploidy of some of them. Further hybridisation of the autopolyploids with each other and with the diploids and the formation of allo-polyploids would account for the great diversity of the group, and for the similarities between the species.

VIII. FURTHER RESEARCH.

Several aspects of this investigation appear to offer scope for further research. It is hoped that it will be possible to carry out additional experimental work in the near future. The investigations envisaged are summarised below:-

1. Insufficient work was done on the soil conditions which campestris, multiflora and congesta favour in the field; a few readings of pH and of soil moisture content were made, but they were very incomplete, and so were omitted from this thesis. More complete analyses of soils from populations of each of the species will be made.

2. The reversal of the relative sizes of multiflora and of congesta when grown under cultivated conditions, compared with the wild plants, should be investigated further. The most important variable condition seems to be soil moisture content, and an attempt will be made to grow clones of multiflora and congesta in a range of soils from dry to saturated. Other variables which might be investigates are soil pH and the effect of shading.

3. The results obtained from the comparison of the morphological characteristics of the plants with the chromosome number proved to be of considerable interest; it seems to be desirable to compare a much larger sample of plants in this way.

4. The nature of the inflorescence of multiflora and congesta is a problem which would benefit by further study. A series of crosses between these species would have to be carried out, and the progeny grown under uniform conditions and analysed morphologically.

A series of known octoploid congesta and of known hexaploid *multiflora* will be grown, and the crosses outlined below will be made. In addition, it would seem to be desirable to self at least one inflorescence in each plant.

a) Plants of *multiflora* will be crossed with other plants of the same species from different sources, to determine the range of variation of the species; the same will be done for *congesta*.

b) Plants of *multiflora* will be crossed with plants of *congesta*. If possible, some of these will have come from the same population, and others from widely separated populations.

These crosses should result in five groups of seed:- selfed *multiflora*, *multiflora* x *multiflora*, *multiflora* x *congesta*, *congesta* x *congesta* and selfed *congesta*. The seeds would be germinated in the greenhouse, and the seedlings transferred to small individual pots after one or two month's growth; the pots would be put into cold frames to harden off. About 200 plants of the *multiflora* x *congesta* group would be grown, with perhaps 50 plants of each of the other groups. It would probably not be possible to obtain chromosome counts for all these plants in one season, but an inflorescence from each could be pressed, and the morphological analysis carried out. The available chromosome numbers could be compared with this analysis, and subsequent counts could be added as they were made.

5. An attempt should be made to obtain artificial hybrids between *campestris* and *multiflora* or *congesta*.

IX. SUMMARY

1. Luzula campestris (L) DC. as described in Buchenau's Monograph of the Juncaceae is morphologically very diverse; to the twenty varieties described in this work, six more have been added since 1906.

2. The geographical distributions of these taxa are different; many of them overlap, but some cover only a very limited area.

3. The taxa found in Europe are ecologically separated. Their morphology has been more closely examined, and they are found to fall into six quite distinct groups: sudetica, pallescens, campestris, multiflora, campestris and congesta. A small proportion of plants could not be assigned to any taxon, and must be considered as possible hybrids or as intermediate forms.

   The flowering time of campestris is two or three months before that of the other taxa.

4. Three of the taxa are very common in Britain: campestris, multiflora and congesta. They are ecologically separated, campestris growing in dry grassland, multiflora in woods and congesta in moors and bogs.

5. Detailed examination of the morphology of these three taxa shows that they remain more or less distinct in the field, but that they do merge into each other to some extent. The number of plants intermediate between congesta and multiflora is much

greater than the number between campestris and either of them.

6. The three taxa mentioned above were grown under identical conditions in the experimental garden. The morphological differences were maintained in the floral characters, and the differences between campestris and the other taxa in the vegetative characters were emphasised.

7. Chromosome counts were obtained from seedlings and from plants grown in cultivation. The numbers obtained were:-

pallescens	2n = 12	diploid
campestris	2n = 12	diploid
multiflora	2n = 36	hexaploid
congesta	2n = 48	octoploid
multiflora x congesta	2n = 42	heptaploid

8. The evidence from the morphology, ecology and cytology of the British material suggests that specific rank should be given to all three.

9. If (campestris) multiflora and congesta are recognised at specific rank, it seems to be reasonable that most of the other varieties should receive the same treatment. Specific rank is therefore proposed for all the varieties of L. campestris in Buchenau, with the exception of flaccida, debilis and calabra, of which insufficient material was available. Specific rank is also recommended for L. echinata, L. bulbosa and probably also for L. kobaysii, L. kjellmanniana and L. cusickii.

10. Although the taxa warrant specific rank, some recognition of their affinities should be made. They should perhaps therefore be considered as an aggregate species, L. campestris agg., which is composed of a polyploid complex of related species.

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APPENDIX I.

Tables of maxima, means and minima of diagnostic characters for every population from which a mass gathering was obtained.

Figures 53 - 77, ogives of X, Y and Z for these populations are included with the tables.

I A

Date : 27/7/55 Altitude : 500 ft.

Locality : Fortingal, Perthshire. Grid Reference : 27/726465

Habitat : Dry pasture; 15 degree slope to east. Agrostis tenuis dominant, with Holcus lanatus, Anthoxanthum odoratum and Euphrasia sp. frequent.

Character	max.	mean	min.	standard deviation
H	19.0 cm.	13.4 cm.	8.5 cm.	3.33 cm.
L	7.5 cm.	4.53 cm.	2.2 cm.	1.23 cm.
B	0. 25 cm.	0.195 cm.	0.12 cm.	0.049 cm.
Z	51	39	24	
s/w	1.61	1.270	1.04	0.117
a + f	1.96 mm.	1.586 mm.	1.08 mm.	0.202 mm.
$\frac{a}{a + f}$	0.768	0.6223	0.422	0.0732
F	10-20	c. 12	1-5	
Sp	4	3	1	
X	112	74	58	
S	1.06 cm.	0.556 cm.	0.15 cm.	0.247 mm.
s x w	137	108.5	64	16.1
P	3.75 mm.	3.04 mm.	1.95 mm.	0.338 mm.
Y	97	79	48	

I B

Date : 28/7/55 Altitude :500 ft.

Locality : Fortingal. Grid reference : 27/726465

Habitat : Pasture below I A; damper, with longer grass and less *Pteridium*; slope 10 - 15 degrees. *Anthoxanthum odoratum*, *Potentilla erecta* and *Succisa pratensis* all abundant, with frequent *Nardus stricta*, *Galium verum* and *Plantago lanceolata*.

Character	max.	mean	min.	standard deviation
H	36.0 cm.	25.4 cm.	13.0 cm.	4.95 cm.
L	10.1 cm.	7.67 cm.	4.1 cm.	1.85 cm.
B	0.41 cm.	0.308 cm.	0.15 cm.	0.0707 cm.
Z	80	66.5	36	
s/w	1.73	1.468	1.20	0.1256
a + f	2.17 mm.	1.493 mm.	1.22 mm.	0.175 mm.
$\frac{a}{a+f}$	0.687	0.5573	0.462	0.0494
F	36-40	c. 25	11-15	
Sp	7	4	2	
X	120	101	63	
s x w	140	116.4	66	15.1
S	1.44 cm.	0.721 cm.	0.16 cm.	0.314 cm.
P	3.65 mm.	3.096 mm.	2.55 mm.	0.242 mm.
Y	107	82	46	

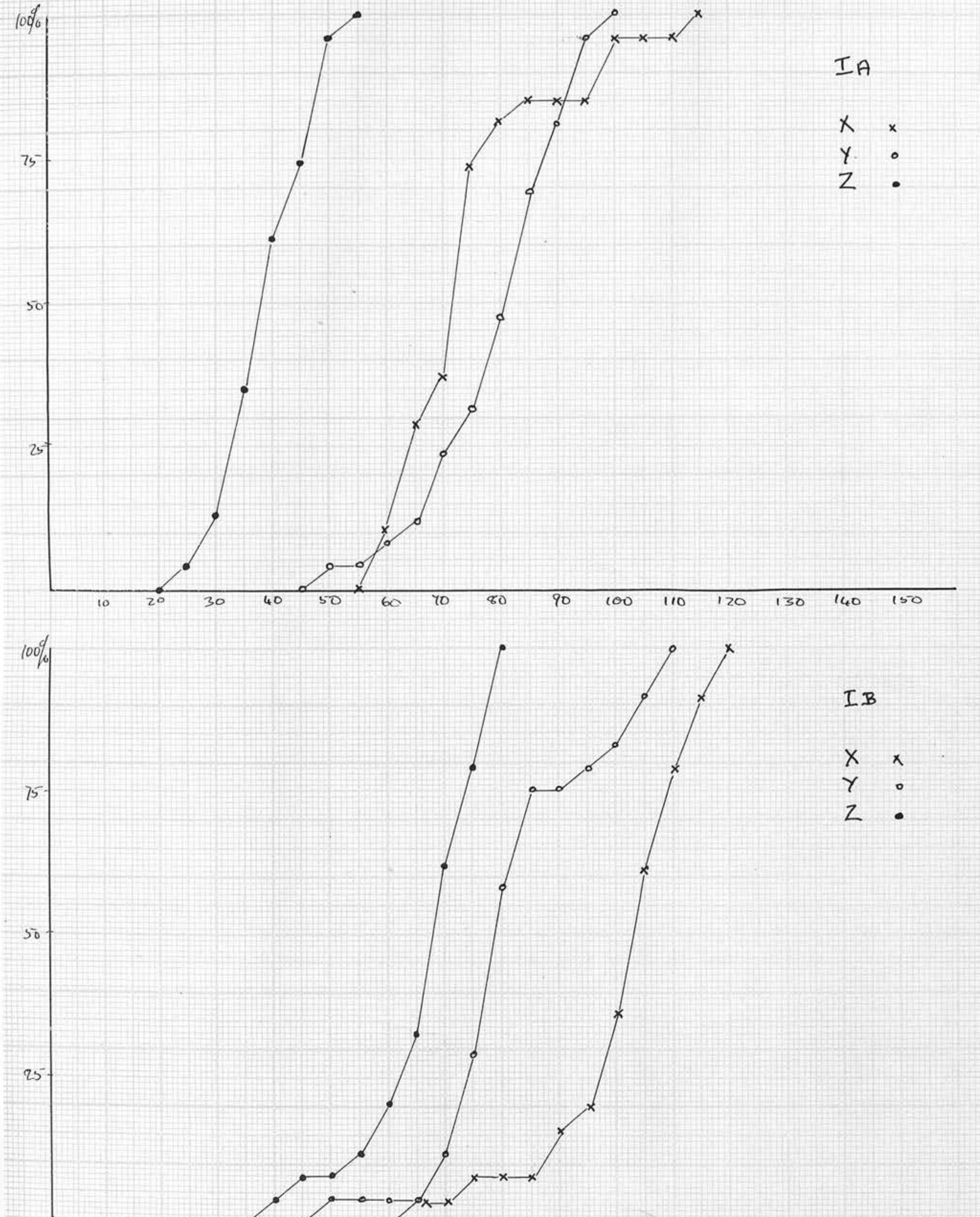

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Fig. 53 a and b.

I C

Date : 28/7/55 Altitude : 500 ft.

Locality : Fortingal. Grid Reference : 27/726465

Habitat : Damp flush in field, alongside A and B; sloping east at 10 - 15 degrees. <u>Molinia caerulea</u>, <u>Anthoxanthum odoratum</u>, <u>Holcus lanatus</u> and <u>Juncus articulatus</u> all abundant; <u>Succisa pratensis</u>, <u>Potentilla erecta</u> and <u>Plantago lanceolata</u> frequent.

Character	max.	mean	min.	standard deviation
H	56.5 cm.	34.4 cm.	21.0 cm.	7.76 cm.
L	14.7 cm.	8.82 cm.	4.7 cm.	2.18 cm.
B	0.44 cm.	0.309 cm.	0.19 cm.	0.060 cm.
Z	105	73	48	
s/w	1.66	1.478	1.28	0.0895
a + f	2.19 mm.	1.393 mm.	1.10 mm.	0.201 mm.
$\frac{a}{a + f}$	0.687	0.5093	0.371	0.0713
F	46-50	c. 22	11-15	
Sp	7	4	2	
X	123	105	60	
S	1.17 cm.	0.524 cm.	0.13 cm.	0.343 cm.
s x w	148	124.3	94	15.7
P	4.10 mm.	3.082 mm.	2.20 mm.	0.398 mm.
Y	119	89	59	

II A

Date : 27/7/55 Altitude: 600 ft.

Locality : Glen Lyon, near Fortingal. Grid Reference : 27/707472

Habitat : Moist woodland, shade not very dense. Growing with _Poa nemoralis_, _Pteridium aquilinum_, _Geum urbanum_, _Succisa pratensis_ and _Lysimachia nemorum_.

Character	max.	mean	min.	standard deviation
H	53.0 cm.	37.1 cm.	25.0 cm.	8.01 cm.
L	14.4 cm.	10.44 cm.	6.9 cm.	1.92 cm.
B	0.44 cm.	0.304 cm.	0.20 cm.	0.078 cm.
Z	99	78	62	
s/w	1.74	1.511	1.42	0.082
a + f	1.81 mm.	1.431 mm.	1.08 mm.	0.197 mm.
$\frac{a}{a+f}$	0.673	0.4798	0.361	0.0827
F	46-50	c. 28	16-20	
Sp	7	5	3	
X	130	113	90	
S	2.65 cm.	1.259 cm.	0.19 cm.	0.728 cm.
s x w	148	104.5	73	18.7
P	3.85 mm.	3.026 mm.	2.05 mm.	0.447 mm.
Y	105	72	41	

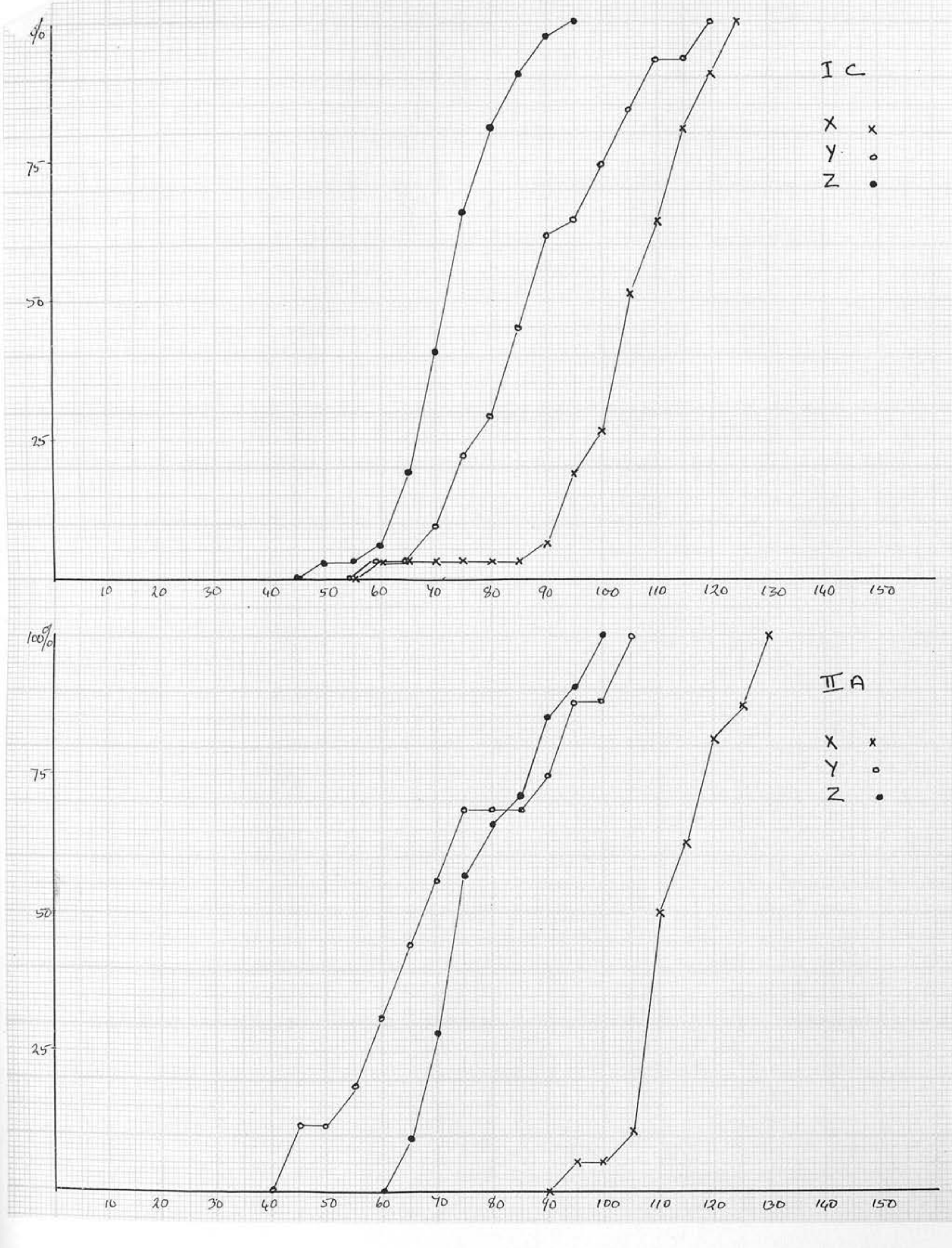
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fig. 54 a and b.

II B

Date : 27/7/55 Altitude : 600 ft.

Locality : Glen Lyon. Grid Reference : 27/708471

Habitat : Bog in open space in mixed wood. Growing with Juncus acutiflorus, J. effusus and J. squarrosus; also with Eriophorum vaginatum, Holcus lanatus and Anthoxanthum odoratum.

Character	max.	mean	min	standard deviation
H	54.0 cm.	37.9 cm.	19.0 cm.	7.25 cm.
L	21.0 cm.	13.92 cm.	8.0 cm.	2.59 cm.
B	0.50 cm.	0.304 cm.	0.20 cm.	0.065 cm.
Z	100	85	66	
s/w	1.85	1.607	1.44	0.086
a + f	1.84 mm.	1.403 mm.	1.12 mm.	0.161 mm.
$\frac{a}{a + f}$	0.582	0.4619	0.305	0.0623
F	56-60	c. 26	16-20	
Sp	8	4	3	
X	136	116	95	
S	1.01 cm.	0.356 cm.	0.12 cm.	0.247 cm.
s x w	152	131.4	105	11.7
P	3.95 mm.	3.319 mm.	2.45 mm.	0.319 mm.
Y	123	100	70	

II C

Date : 27/7/55 Altitude : 600 ft.

Locality : Glen Lyon. Grid Reference : 27/710471

Habitat : Pasture on dry, fairly steep slope facing north; open space in wood. Growing with Agrostis tenuis, Anthoxanthum odoratum, Holcus lanatus, Potentilla erecta and Campanula rotundifolia.

Character	max.	mean	min.	standard deviation
H	30.0 cm.	19.1 cm.	11.5 cm.	4.64 cm.
L.	11.5 cm.	6.18 cm.	3.3 cm.	4.64 cm.
B	0.28 cm.	0.182 cm.	0.09 cm.	0.049 cm.
Z	73	52	32	
s/w	1.39	1.253	1.15	0.061
a + f	2.24 mm.	1.74 mm.	1.33 mm.	0.212 mm.
$\frac{a}{a+f}$	0.743	0.6397	0.552	0.0594
F	21-25	c. 17	6-10	
Sp	5	4	2	
X	90	71	56	
S	1.52 cm.	0.757 cm.	0.19 cm.	0.334 cm
s x w	147	122.2	95	11.4
P	4.10 mm.	3.405 mm.	3.00 mm.	0.317 mm.
Y	105	87	67	

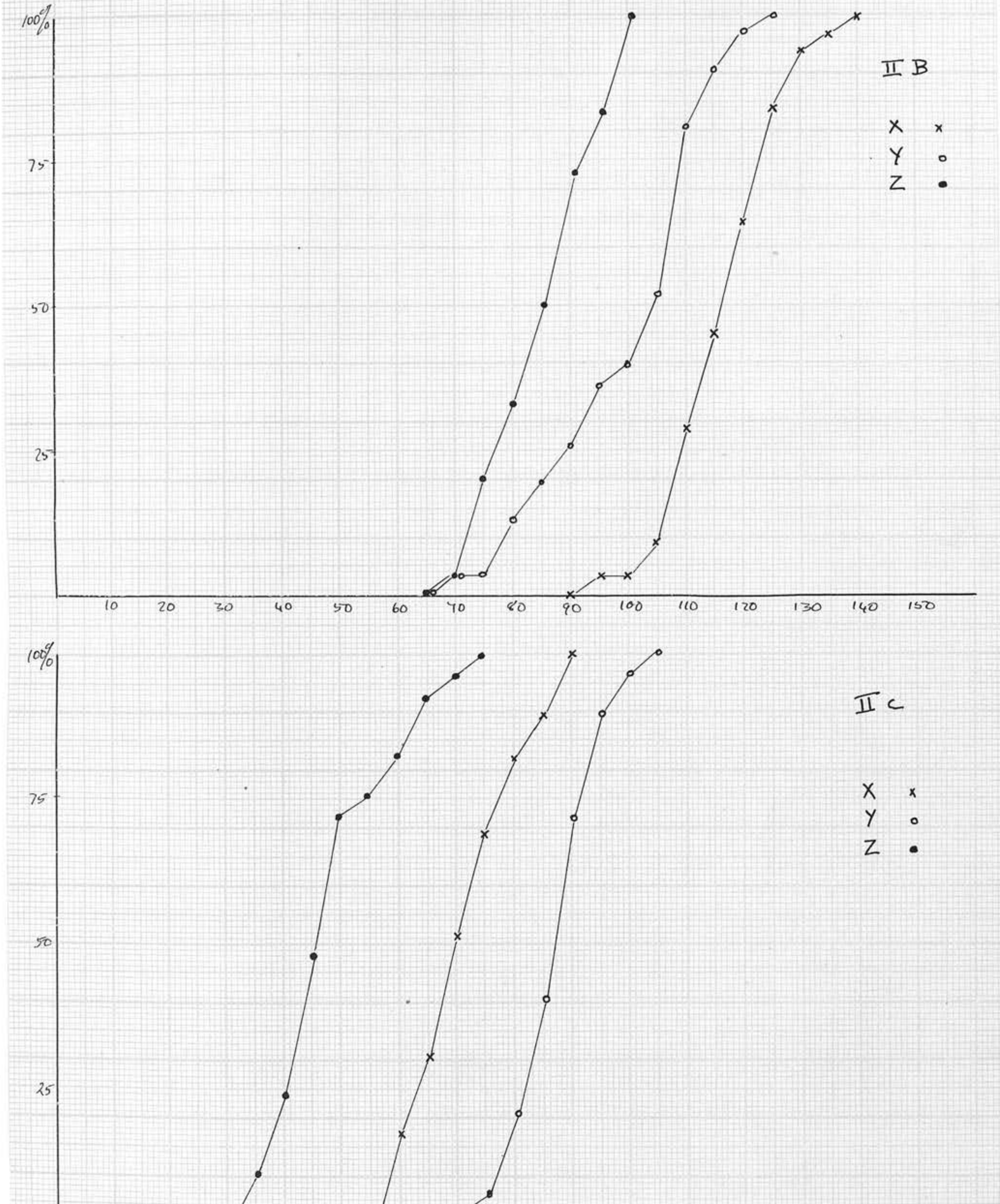
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Fig. 55 a and b

II D

Date : 27/7/55 Altitude : 500 ft.

Locality : Glen Lyon. Grid Reference : 27/720477 to 27/728475

Habitat : At edges of wood, and along path through it; the plants were collected at intervals for a distance of about $\frac{1}{2}$ mile along the path. Generally growing in the damper areas of the wood, associated with Juncus spp., Poa nemoralis etc.

Character	max.	mean	min.	standard deviation
H	55.0 cm.	35.9 cm.	16.0 cm.	8.8 cm.
L	18.5 cm.	10.50 cm.	6.5 cm.	3.10 cm.
B	0.43 cm.	0.323 cm.	0.19 cm.	0.082 cm.
Z	110	78	53	
s/w	1.70	1.522	1.39	0.084
a + f	1.69 mm.	1.343 mm.	1.08 mm.	0.143 mm.
$\frac{a}{a + f}$	0.600	0.4723	0.353	0.0575
F	41-45	c. 25	11-15	
Sp	7	4	2	
X	131	112	101	
s x w	151	116.5	67	20.9
S	1,66 cm.	0.645 cm.	0.15 cm.	0.534 cm.
P	3.90 mm.	3.153 mm.	2.45 mm.	0.463 mm.
Y	118	86	47	

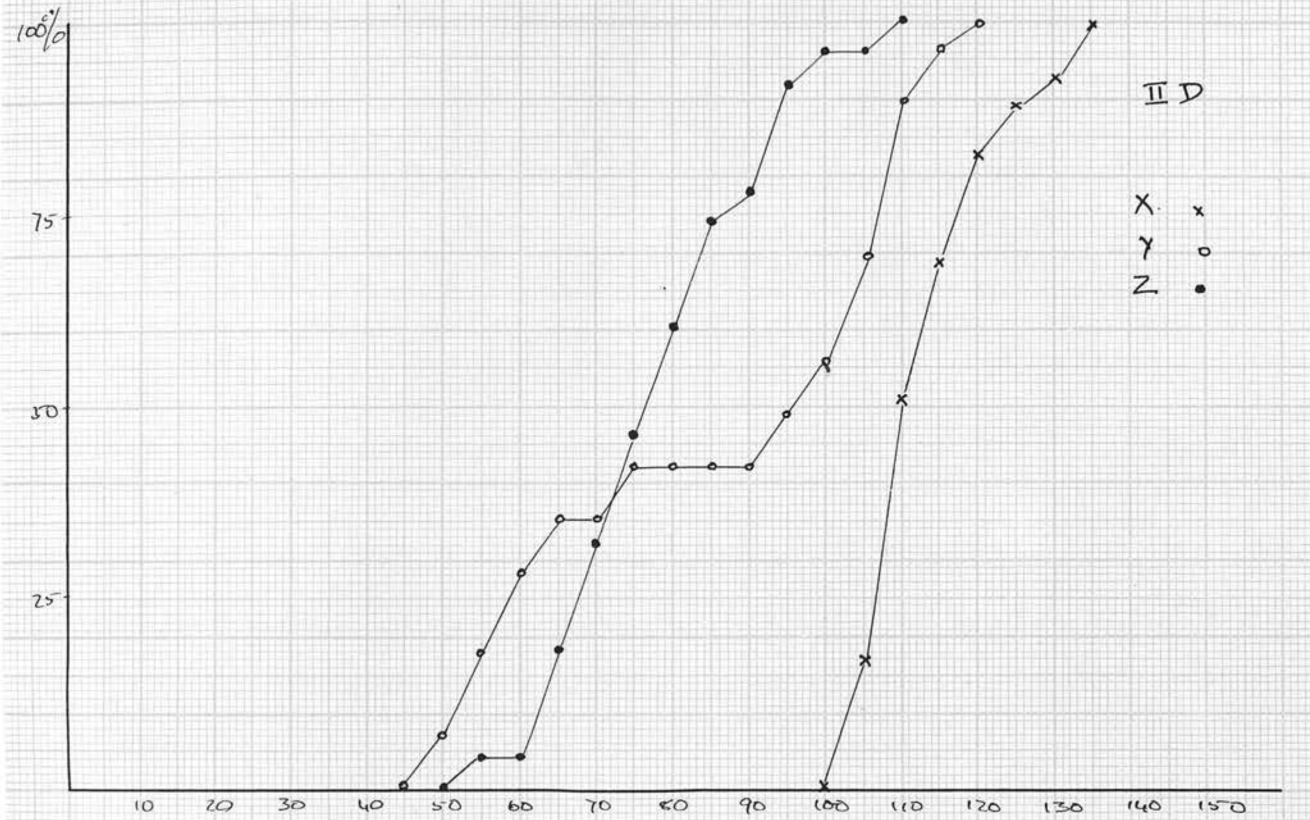
II F (i)

Date : 3/8/55 Altitude : 500 ft.

Locality : Glen Lyon. Grid Reference : 27/716477

Habitat : Bog on more or less level glacial terrace. *Myrica gale* dominant, with abundant *Juncus acutiflorus* and also *Cirsium palustre*, *Filipendula ulmaria*, *Narthecium ossifragum*, *Potentilla erecta* and *Succisa pratensis*.

Character	max.	mean	min.	standard deviation
H	67.0 cm.	54.3 cm.	39.0 cm.	7.83 cm.
L	21.0 cm.	14.02 cm.	10.5 cm.	2.62 cm.
B	0.60 cm.	0.416 cm.	0.26 cm.	0.093 cm.
Z	125	101	81	
s/w	1.62	1.554	1,46	0.390
a + f	1.81 mm.	1.328 mm.	0.91 mm.	0.179 mm.
$\frac{a}{a + f}$	0.505	0.4204	0.323	0.0491
F	56-60	c. 35	16-20	
Sp	7	5	3	
X	133	122	108	
S	0.25 cm.	0.204 cm.	0.115 cm.	0.093 cm.
s x w	160	131.8	107	13.7
P	3.95 mm.	3.392 mm.	2.90 mm.	0.27 mm.
Y	121	107	96	



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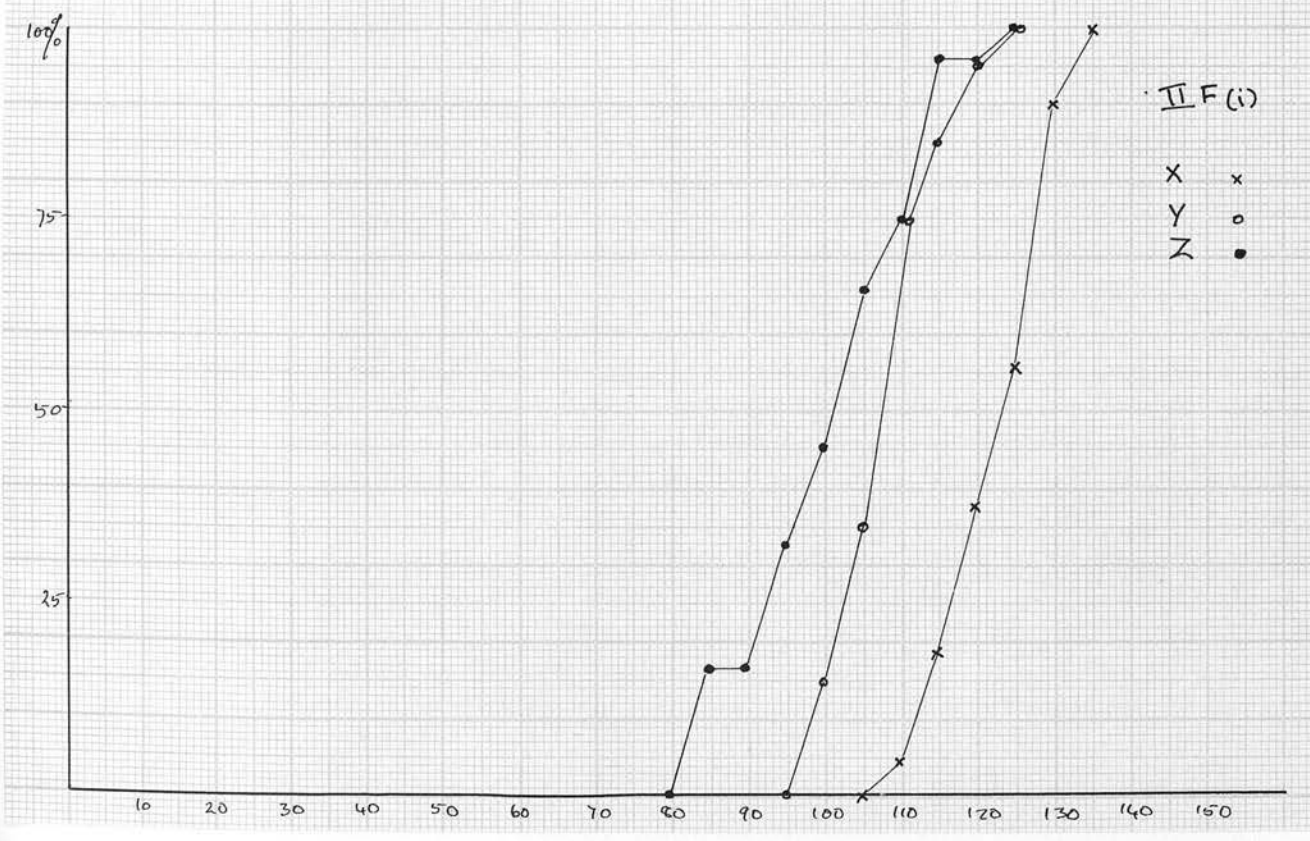

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Fig. 56 a and b

II F (ii)

Date : 3/8/55 Altitude : 500 ft.

Locality : Glen Lyon. Grid Reference : 27/716477

Habitat : Edge of bog, very moist. Juncus acutiflorus dominant; Carex echinata abundant, with frequent Potentilla erecta, Epilobium palustre and Anthoxanthum odoratum. Myrica rare.

Character	max.	mean	min.	standard deviation
H	68.0 cm.	47.7 cm.	36.0 cm.	8.8 cm.
L	18.5 cm.	11.88 cm.	7.5 cm.	2.86 cm.
B	0.52 cm.	0.363 cm.	0.23 cm.	0.070 cm.
Z	111	90	72	
s/w	1.62	1.543	1.45	0.047
a + f	1.75 mm.	1.329 mm.	0.97 mm.	0.205 mm.
$\frac{a}{a + f}$	0.545	0.4377	0.289	0.0765
F	41-45	c. 30	21-25	
Sp	7	5	3	
X	142	119	101	
S	0.23 cm.	0.191 cm.	0.13 cm.	0.025 cm.
s x w	148	129.4	111	10.2
P	3.95 mm.	3.231 mm.	2.55 mm.	0.346 mm.
Y	120	104	90	

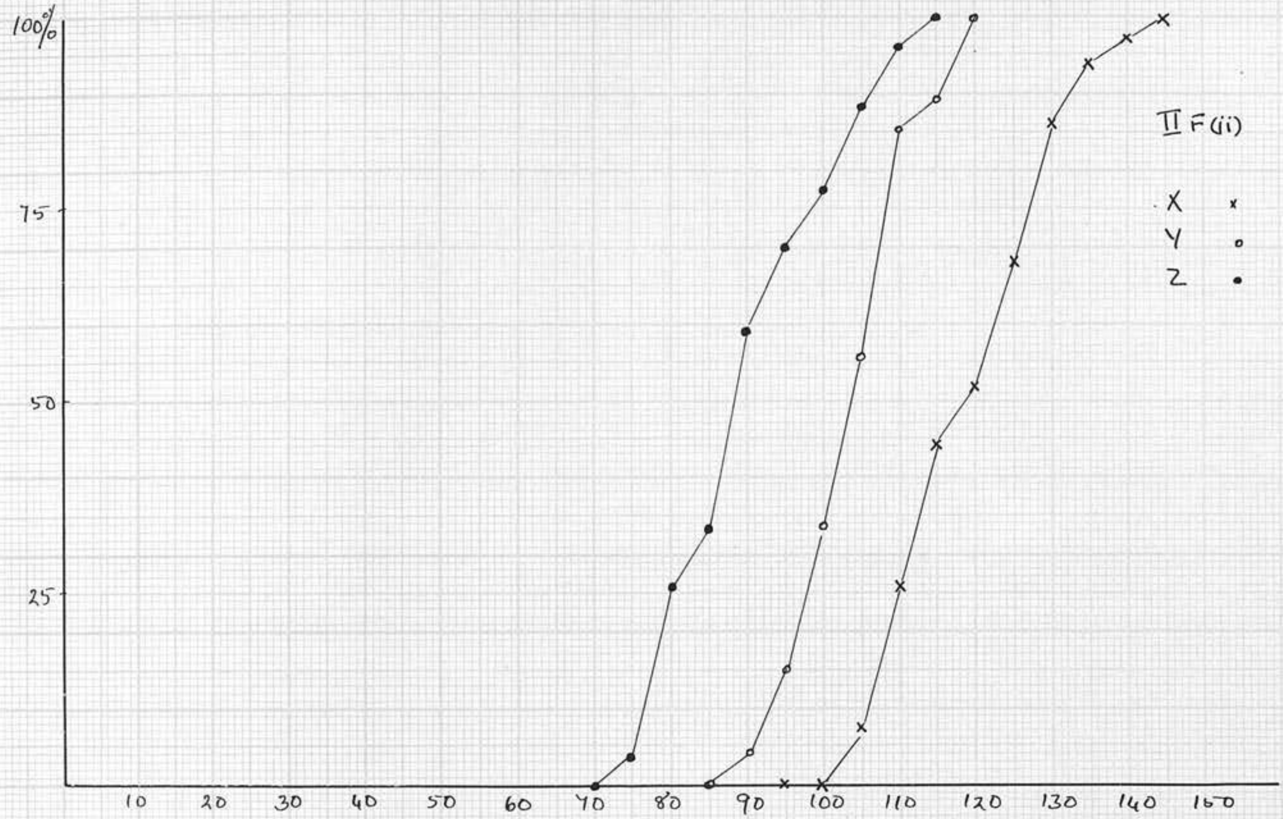
II F (iii)a

Date : 3/8/55 Altitude : 500 ft.

Locality : Glen Lyon. Grid Reference : 27/716477

Habitat : Foot of grassy slope above bog; facing north. _Potentilla erecta_ and _Galium saxatile_ abundant; _Anthoxanthum odoratum_, _Festuca rubra_ and _Anemone nemorosa_ frequent.

Character	max.	mean	min.	standard deviation
H	47.0 cm.	30.7 cm.	19.0 cm.	6.6 cm.
L	14.5 cm.	8.97 cm.	5.5 cm.	2.4 cm.
B	0.42 cm.	0.275 cm.	0.17 cm.	0.064 cm.
Z	93	70	48	
s/w	1.74	1.479	1.16	0.154
a + f	2.13 mm.	1.413 mm.	0.93 mm.	0.220 mm.
$\frac{a}{a + f}$	0.714	0.4754	0.291	0.1076
F	31-35	c. 17	6-10	
Sp	5	3	2	
X	122	101	62	
S	1.24 cm.	0.353 cm.	0.13 cm.	0.298 cm.
a x w	154	128.4	100	12.2
P	3.75 mm.	3.25 mm.	2.40 mm.	0.304 mm.
Y	117	99	66	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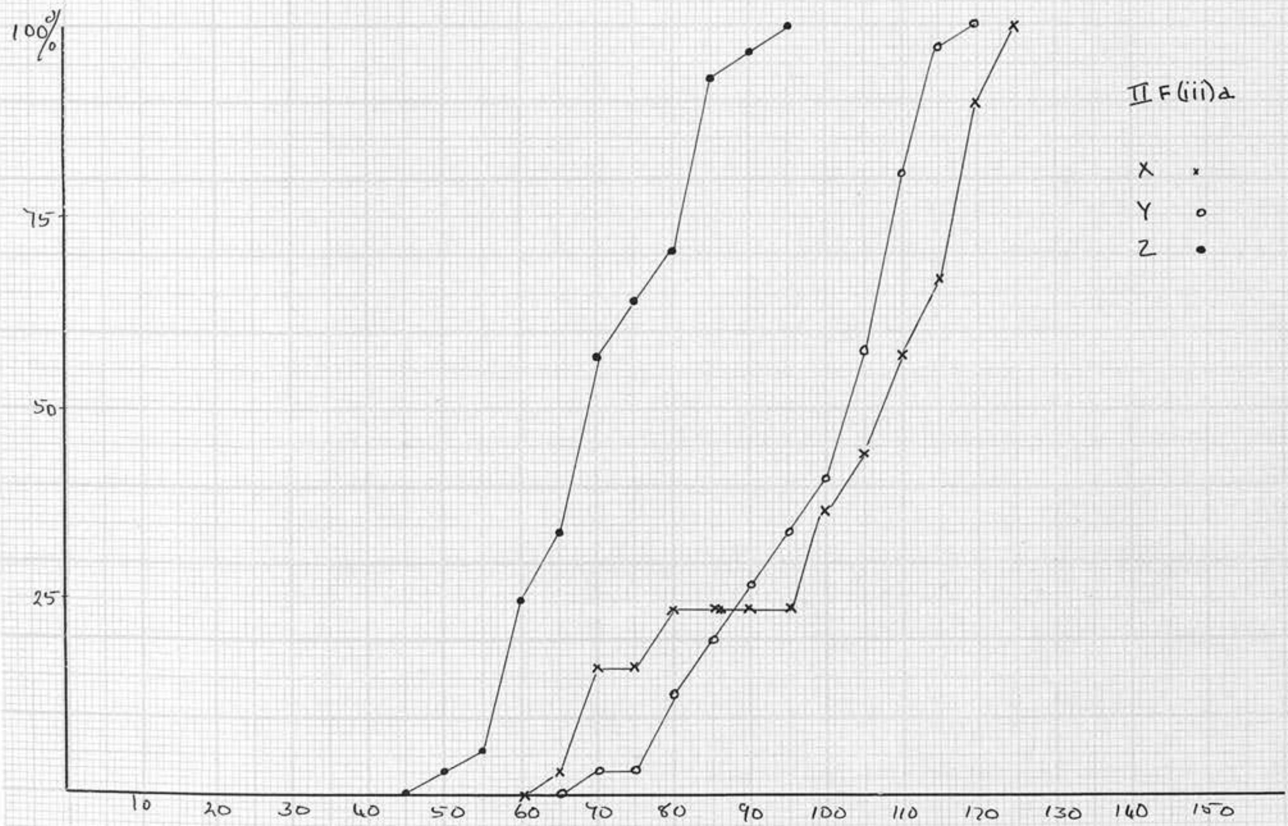
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Fig. 57 a and b

II F (iii)b

Date : 3/8/55 Altitude : 500 ft.

Locality : Glen Lyon. Grid Reference : 27/716477

Habitat : Top of slope above bog. Galium saxatile and Potentilla erecta abundant; Festuca rubra, Agrostis tenuis and Anemone nemorosa frequent.

Character	Max.	mean	min.	standard deviation
H	33.0 cm.	21 cm.	9.0 cm.	6.6 cm.
L	11.0 cm.	5.95 cm.	3.3 cm.	2.80 cm.
Z	77	51	31	
s/w	1.68	1.361	1.09	0.165
a + f	2.19 mm.	1.54 mm.	1.24 mm.	0.23 mm.
$\frac{a}{a + f}$	0.738	0.5577	0.366	0.1226
F	26-30	c. 15	1-5	
Sp	4	3	1	
X	118	85	53	
S	1.01 cm.	0.562 cm.	0.16 cm.	0.352 cm.
s x w	145	115.8	92	13.8
P	3.90 mm.	3.423 mm.	2.80 mm.	0.276 mm.
Y	123	90	69	

II F (iv)

Date : 3/8/55 Altitude : 500 ft.

Locality : Glen Lyon. Grid Reference : 27/716477

Habitat : Level pasture ~~with~~ on second glacial terrace; fairly dry. Festuca rubra and Galium saxatile abundant; Potentilla erecta and Anthoxanthum odoratum very frequent, also Campanula rotundifolia, Trifolium repens and Agrostis tenuis.

Character	max.	mean	min.	standard deviation
H	27.0 cm.	14.3 cm.	4.0 cm.	5.43 cm.
L	8.0 cm.	4.31 cm.	2.2 cm.	1.26 cm.
B	0.24 cm.	0.174 cm.	0.12 cm.	0.031 cm.
Z	54	39	17	
s/w	1.46	1.206	1.04	0.077
a + f	2.17 mm.	1.618 mm.	1.24 mm.	0.198 mm.
$\frac{a}{a + f}$	0.766	0.661	0.549	0.0594
F	21-25	c. 13	6-10	
Sp	4	3	2	
X	87	67	47	
S	1.60 cm.	0.761 cm.	0.24 cm.	0.286 cm.
s x w	144	103.4	61	17.02
P	4.30 mm.	3.246 mm.	2.55 mm.	0.366 mm.
Y	104	77	64	

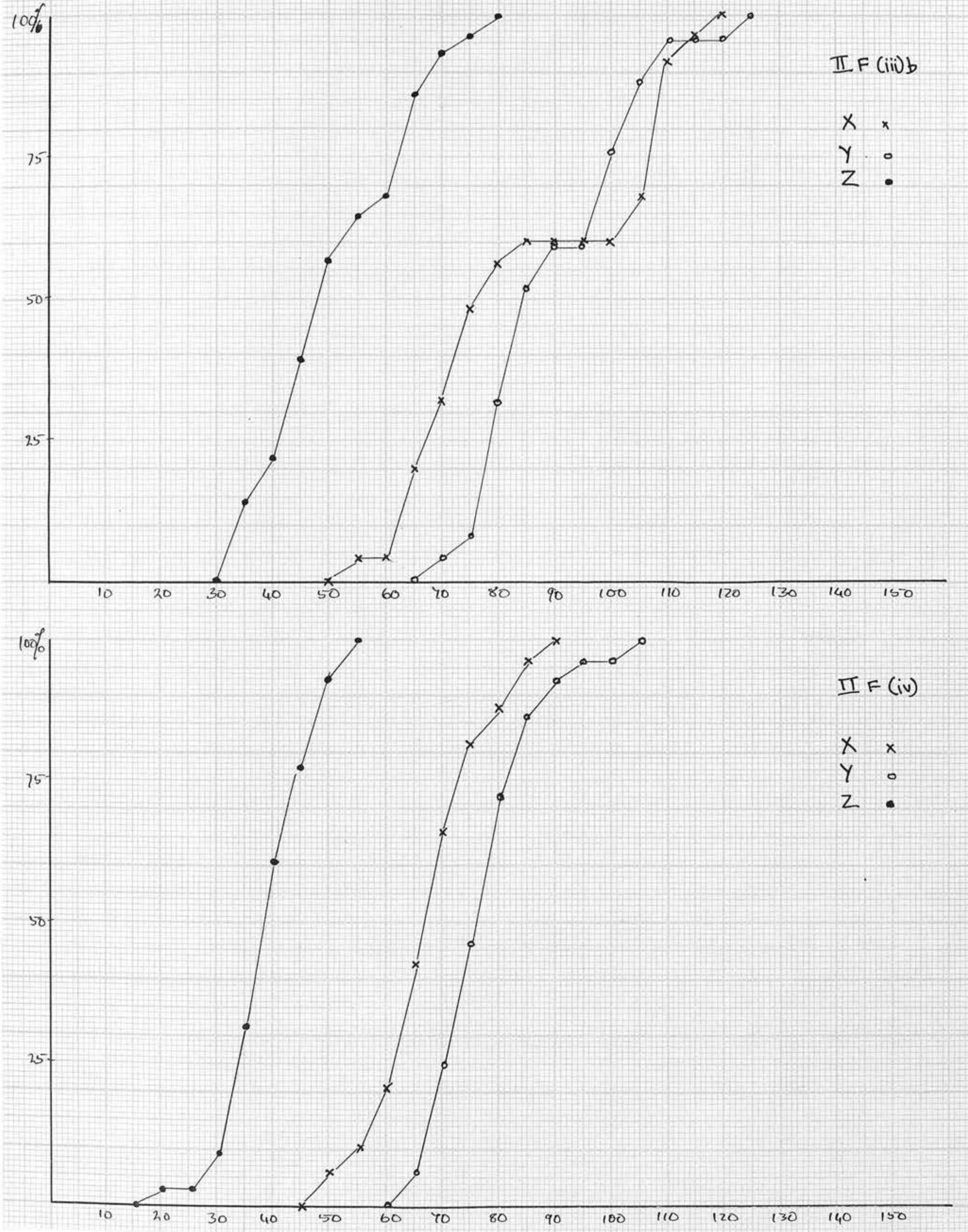

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Fig. 58 a and b

III A

Date : 28/7/55 Altitude : c. 700 ft.

Locality : Fortingal. Grid Reference : 27/742461

Habitat : Alnus-Corylus wood, with Betula; on slope facing north. Juncus articulatus, Carex remota and Cirsium palustre abundant.

Filipendula ulmaria, Ranunculus flammula, Juncus effusus and Poa trivialis frequent.

Character	max.	mean	min.	standard deviation
H	62.0 cm.	43.6 cm.	28.0 cm.	9.1 cm.
L	22.0 cm.	13.76 cm.	8.0 cm.	3.15 cm.
B	0.43 cm.	0.298 cm.	0.20 cm.	0.056 cm.
Z	109	86	64	
s/w	1.80	1.582	1.47	0.080
a + f	1.98 mm.	1.472 mm.	1.22 mm.	0.166 mm.
$\frac{a}{a + f}$	0.558	0.4280	0.309	0.0596
F	71-75	c. 40	16-20	
X	150	125	107	
S	2.72 cm.	1.343 cm.	0.21 cm.	0.572 cm.
s x w	142	97.3	75	15.2
P	4.15 mm.	2.87 mm.	2.35 mm.	0.409 mm.
Y	112	61	45	

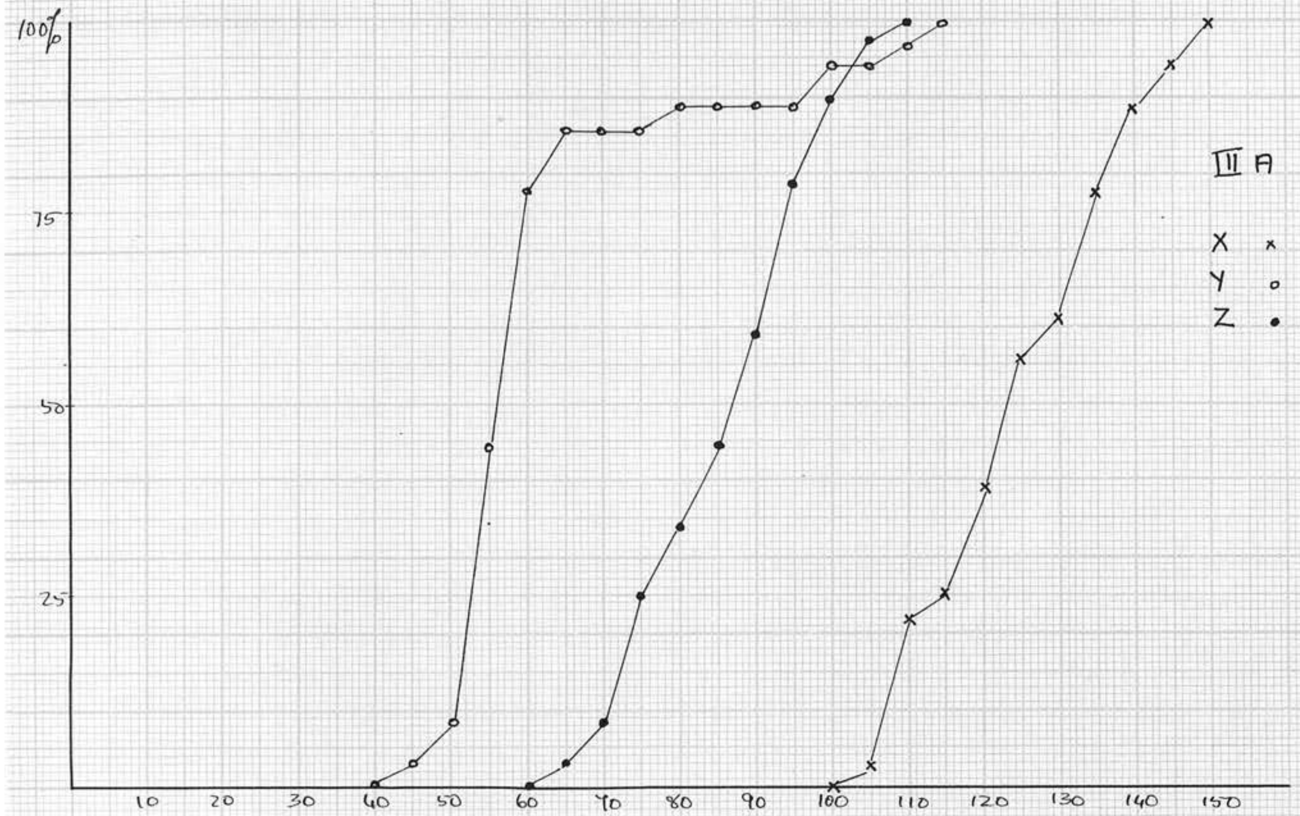
III B

Date : 28/7/55 Altitude : 5-600 ft.

Locality : Fortingal. Grid Reference : 27/742461

Habitat : Damp flush in wood; open and facing north, farther down slope than III A. Growing with Juncus articulatus, J. conglomeratus, J. bulbosus, Galium palustre and Filipendula ulmaria.

Character	max.	mean	min.	standard deviation
H	55.0 cm.	34.1 cm.	21,0 cm.	7.85 cm.
L	17.5 cm.	11.21 cm.	5.3 cm.	3.32 cm.
B	0.43 cm.	0.275 cm.	0.19 cm.	0.067 cm.
Z	106	73	47	
s/w	1.78	1.477	1.17	0.132
a + f	1.98 mm.	1.484 mm.	1.10 mm.	0.199 mm.
$\frac{a}{a+f}$	0.673	0.4723	0.328	0.0717
F	61-65	c. 30	16-20	
Sp	9	4	2	
X	142	111	88	
S	1.91 cm.	1.130 cm.	0.68 cm.	0.284 cm.
s x w	137	105.5	75	15.1
P	3.60 mm.	2.846 mm.	2.35 mm.	0.267 mm.
Y	79	64	48	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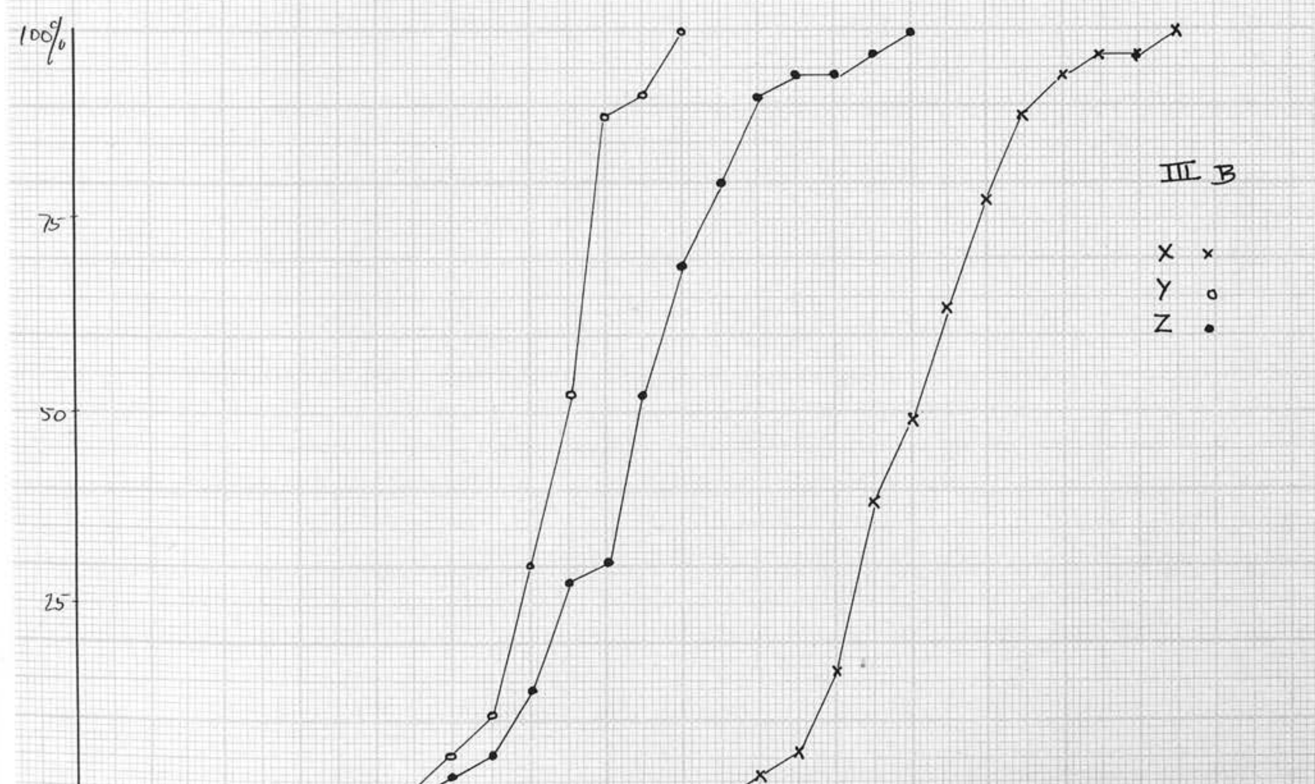
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Fig. 59 a and b

III C

Date : 28/7/55 Altitude : 450 ft.

Locality : Fortingal. Grid Reference : 27/740463

Habitat : Ditch at roadside; mainly damp, but with dry patches. growing with *Juncus conglomeratus*, *J.articulatus*, *Filipendula ulmaria*, *Anthoxanthum odoratum* and *Agrostis tenuis*.

Character	max.	mean	min.	standard deviation
H	52.0 cm.	36.6 cm.	21.0 cm.	9.2 cm.
L	15.5 cm.	10.29 cm.	4.5 cm.	2.73 cm.
B	0.37 cm.	0.265 cm.	0.19 cm.	0.054 cm.
Z	95	74	47	
s/w	1.67	1.441	1.10	0.138
a + f	1.69 mm.	1.373 mm.	1.05 mm.	0.179 mm.
$\frac{a}{a+f}$	0.690	0.4923	0.339	0.0924
F	56-60	c. 30	11-15	
Sp	9	5	3	
X	139	111	62	
S	2.31 cm.	1.138 cm.	0.51 cm.	0.365 cm.
s x w	159	104.5	75	14.8
P	3.25 mm.	2.983 mm.	2.15 mm.	0.248 mm.
Y	90	67	54	

III D

Date : 29/7/55 Altitude : 450 ft.

Locality : Fortingal. Grid Reference : 27/738463

Habitat : Ditch at roadside; similar type of habitat to III C.

Associated with <u>Juncus</u> spp.

Character	max.	mean	min.	standard deviation
H	67.5 cm.	43.9 cm.	22.0 cm.	11.3 cm.
L	20.5 cm.	13.38 cm.	6.5 cm.	3.12 cm.
B	0.52 cm.	0.31 cm.	0.14 cm.	0.088 cm.
Z	117	87	55	
s/w	1.771	1.482	1.33	0.097
a + f	2.13 mm.	1.491 mm.	1.18 mm.	0.213 mm.
$\frac{a}{a + f}$	0.714	0.4749	0.355	0.0695
F	51-55	c. 30	11-15	
Sp	8	4	2	
X	140	110	95	
S	2.41 cm.	0.437 mm.	0.16 cm.	0.439 cm.
s x w	153	121.9	86	15.4
P	3.95 mm.	3.296 mm.	2.55 mm.	0.379 mm.
Y	117	96	54	

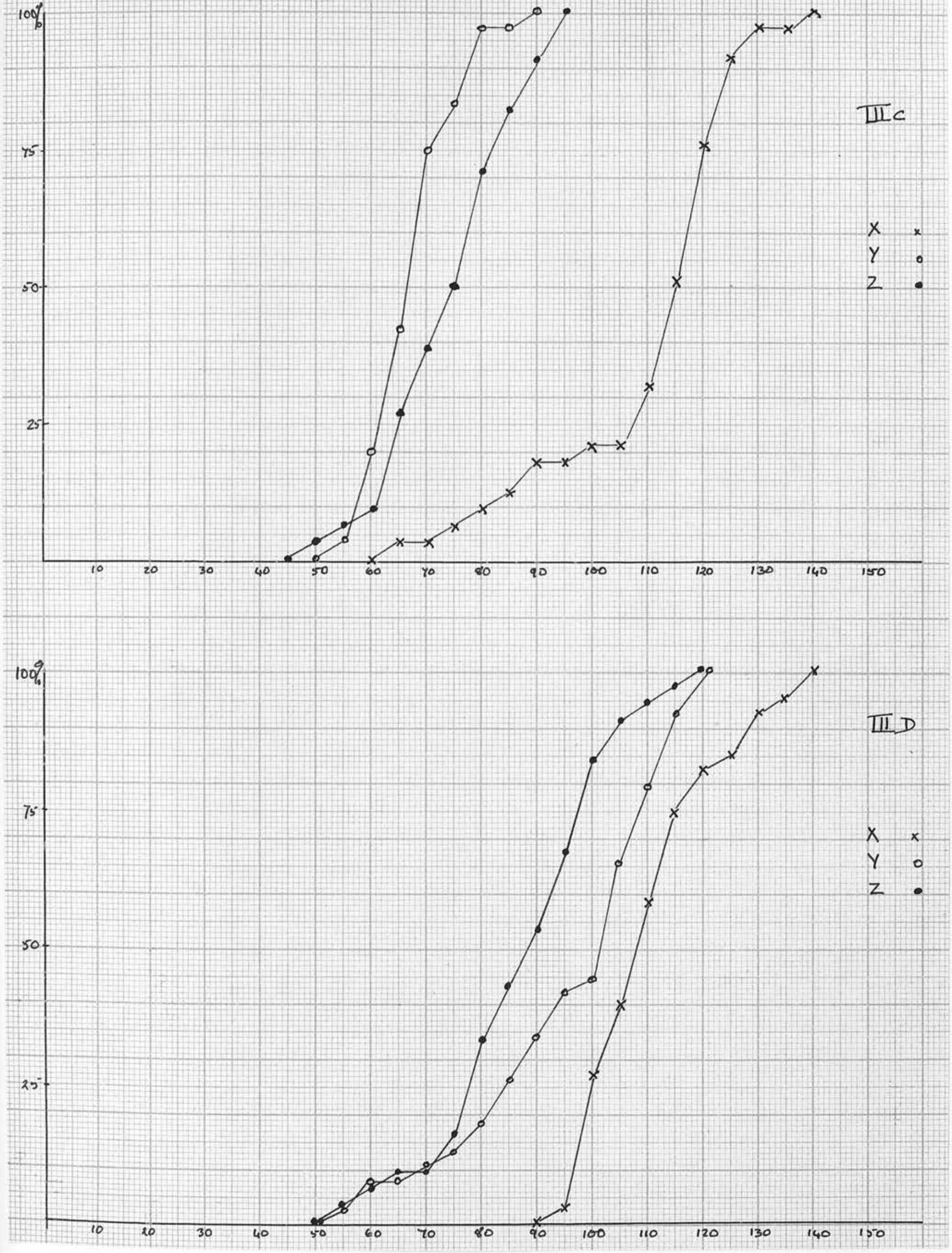

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Fig. 60 a and b

IV A

Date : 31/7/55

Locality : Glen Ogle, Perthshire.

Habitat : Dry pasture with much Calluna and Pteridium, at the edge of small burn. Growing with Festuca ovina, Nardus stricta, Agrostis tenuis, Potentilla erecta, Vaccinium myrtillus and Salix aurita.

Character	max.	mean	min.	standard deviation
H	50.0 cm.	30.5 cm.	17.0 cm.	8.7 cm.
L.	13.1 cm.	8.71 cm.	4.0 cm.	2.49 cm.
B	0.38 cm.	0.257 cm.	0.12 cm.	0.064 cm.
Z	92	67	32	
s/w	1.68	1.504	1.37	0.068
a + f	1.54 mm.	1.306 mm.	1.03 mm.	0.128 mm.
$\frac{a}{a+f}$	0.580	0.4478	0.315	0.0652
F	31-35	c. 18	6-10	
Sp	5	3	1	
X	129	109	93	
S	1.43 cm.	0.407 cm.	0.12 cm.	0.348 cm.
s x w	145	118.3	90	13.3
P	3.90 mm.	3.14 mm.	2.20 mm.	0.372 mm.
Y	115	93	58	

IV B

Date : 31/7/55

Locality : Glen Ogle.

Habitat : Damp bank of burn; sloping at about 20 degrees to north. *Juncus acutiflorus* dominant; *Carex nigra*, *C. pulicaris*, *Saxifraga aizoides*, *Juncus conglomeratus*, *J. bulbosus*, *Cirsium palustre* and *Galium palustre* also present.

Character	max.	mean	min.	standard deviation
H	53.0 cm.	38.5 cm.	24.0 cm.	6.9 cm.
L	16.5 cm.	12.31 cm.	6.1 cm.	2.71 cm.
B	0.42 cm.	0.300 cm.	0.18 cm.	0.047 cm.
Z	100	81	52	
s/w	1.69	1.547	1.21	0.086
a + f	1.73 mm.	1.33 mm.	0.99 mm.	0.178 mm.
$\frac{a}{a + f}$	0.670	0.426	0.289	0.0727
F	31-35	c, 23	11-15	
Sp	6	3-4	2	
X	134	114	69	
S	1.33 cm.	0.471 cm.	0.13 cm.	0.38 cm.
$s \times w^{\frac{2}{3}}$	146	116.8	90	14.6
P	3.60 mm.	3.164 mm.	2.70 mm.	0.229 mm.
Y	118	93	66	

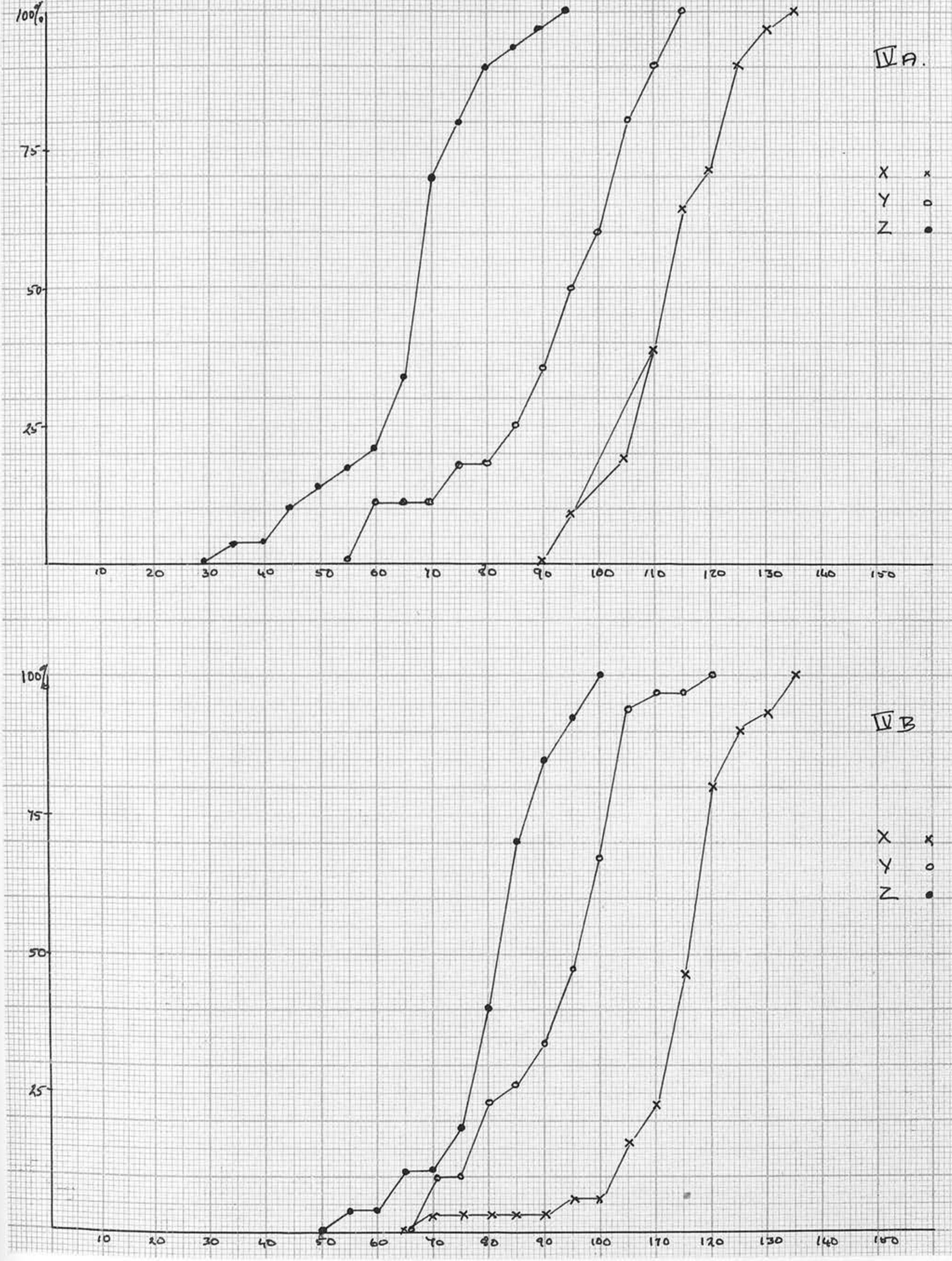
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Fig. 61 a and b

IV C

Date : 31/7/55

Locality : Glen Ogle.

Habitat : Dry pasture, sloping slightly to the north. Growing with Agrostis tenuis, Festuca ovina, Nardus stricta, Juncus squarrosus, Calluna vulgaris and Galium saxatile.

Character	max.	mean	min.	standard deviation
H	40.0 cm.	22.8 cm.	12.0 cm.	6.9 cm.
L	20.7 cm.	9.01 cm.	3.7 cm.	3.62 cm.
B	0.40 cm.	0.264 cm.	0.19 cm.	0.049 cm.
Z	93	63	44	
s/w	1.71	1.528	1.25	0.084
a + f	1.62 mm.	1.344 mm.	1.03 mm.	0.142 mm.
$\frac{a}{a + f}$	0.577	0.4356	0.317	0.0534
F	31-35	c. 17	6-10	
Sp	5	3	2	
X	125	110	81	
S	1.03 cm.	0.244 cm.	0.11 cm.	0.199 cm.
s x w	139	115.5	88	13.8
P	3.80 mm.	3.15 mm.	2.70 mm.	0.225 mm.
Y	112	98	80	

V A

Date : 1/8/55 Altitude : 450 ft.

Locality : South side of Loch Tay, near Killin, Perthshire.

Grid Reference : 27/593332

Habitat : Rough pasture; clearing in bracken, with some shade from single birch tree. Growing with *Agrostis tenuis*, *Festuca rubra*, *Molinia caerulea*, *Galium saxatile* and *Potentilla erecta*.

Character	max.	mean	min.	standard deviation
H	57.0 cm.	34.7 cm.	21,0 cm.	8.6 cm.
L	16.1 cm.	11.15 cm.	8.1 cm.	1.85 cm.
B	0.56 cm.	0.315 cm.	0.16 cm.	0.077 cm.
Z	104	79	62	
s/w	1.73	1.471	1.18	0.101
a + f	2.05 mm.	1.409 mm.	1.03 mm.	0.214 mm.
$\frac{a}{a + f}$	0.747	0.5048	0.344	0.0765
F	46-50	c. 28	11-15	
Sp	9	5	2	
X	129	109	54	
S	1.95 cm.	0.687 cm.	0.15 cm.	0.356 cm.
s x w	150	110.1	77	20.7
P	4.30 mm.	3.041 mm.	2.20 mm.	0.532 mm.
Y	123	79	52	

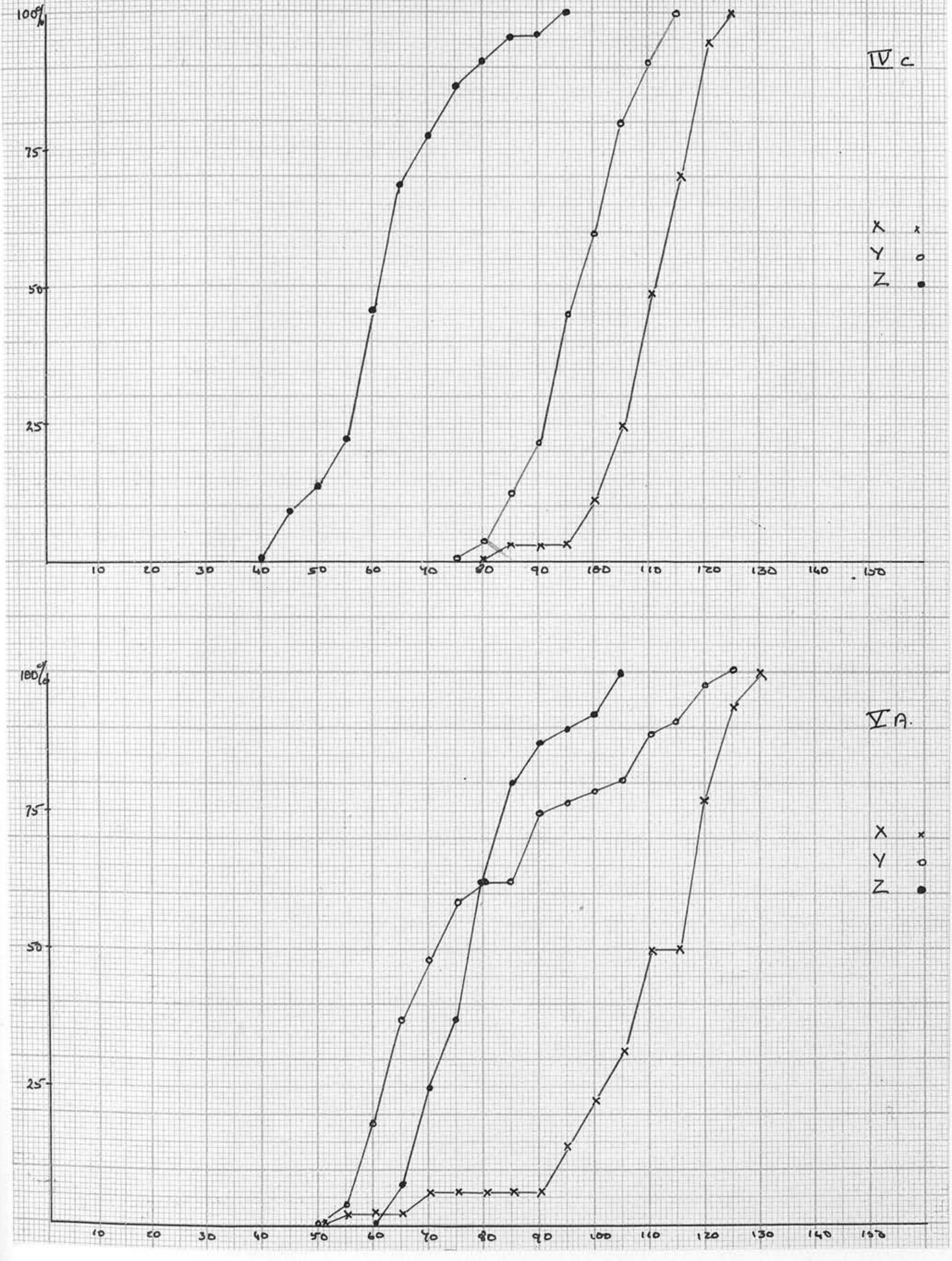

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Fig. 62 a and b

V B

Date : 1/8/55 Altitude : 450 ft.

Locality : South side of Loch Tay. Grid Reference : 27/594332

Habitat : Bog, on a slope facing south. *Juncus acutiflorus* dominant; *J. conglomeratus*, *Cirsium palustre*, *Lychnis flos-cuculi* and *Filipendula ulmaria* also present.

Character	max.	mean	min.	standard deviation
H	69.0 cm.	52.8 cm.	28.0 cm.	10.98 cm.
L	22.5 cm.	15.82 cm.	8.3 cm.	4.23 cm.
B	0.46 cm.	0.325 cm.	0.25 cm.	0.052 cm.
Z	115	97	69	
s/w	1.67	1.496	1.39	0.053
a + f	1.79 mm.	1.471 mm.	1.06 mm.	0.15 mm.
$\frac{a}{a+f}$	0.624	0.5189	0.411	0.0523
F	46-50	c. 26	16-20	
Sp	8	4	2	
X	130	105	66	
S	1.16 cm.	0.403 cm.	0.16 cm.	0.284 cm.
s x w	174	141.96	101	15.5
P	3.95 mm.	3.50 mm.	2.90 mm.	0.309 mm.
Y	120	105	66	

V C

Date : 1/8/55 Altitude : 350 ft.

Locality : South side of Loch Tay. Grid Reference : 27/603337

Habitat : Steep bank on loch side; <u>Luzula</u> not very common.

Character	max.	mean	min.	standard deviation
H	57.0 cm.	37.6 cm.	25.0 cm.	9.58 cm.
L	14.7 cm.	10.49 cm.	4.9 cm.	3.10 cm.
B	0.42 cm.	0.288 cm.	0.18 cm.	0.060 cm.
Z	97	76	52	
s/w	1.77	1.478	1.35	0.108
a + f	1.82 mm.	1.441 mm.	1.10 mm.	0.171 mm.
$\frac{a}{a + f}$	0.633	0.5047	0.400	0.0645
F	56-60	c. 26	11-15	
Sp	8	5	2	
X	136	107	94	
S	2.02 cm.	0.870 cm.	0.15 cm.	0.564 cm.
s x w	158	119.2	101	16.1
P	3.95 mm.	3.263 mm.	2.65 mm.	0.373 mm.
Y	113	84	62	

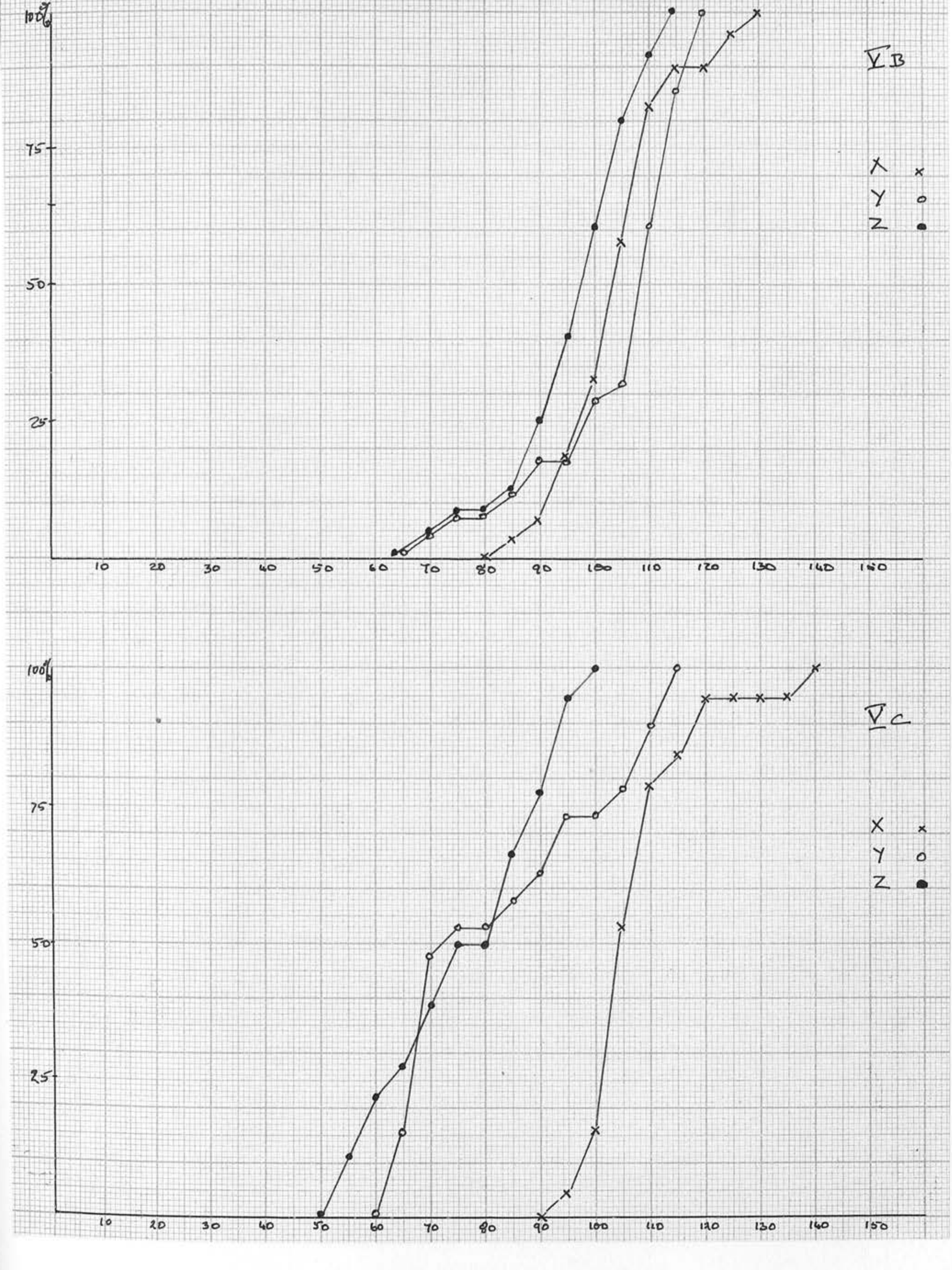
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Fig. 63 a and b

V D

Date : 1/8/55 Altitude : 400 ft.

Locality : South side of Loch Tay. Grid Reference : 27/599335

Habitat : Ditch and bank at roadside. Growing with *Juncus conglomeratus*, *Cirsium palustre*, *Carex panicea*, *Filipendula ulmaria* and *Ranunculus flammula*.

Character	max.	mean	min.	standard deviation
H	60.0 cm.	35.4 cm.	24.0 cm.	8.9 cm.
L	16.2 cm.	11.09 cm.	7.4 cm.	2.32 cm.
B	0.38 cm.	0.260 cm.	0.11 cm.	0.062 cm.
Z	94	74	59	
s/w	1.70	1.532	1.373	0.996
a + f	1.69 mm.	1.276 mm.	1.06 mm.	0.134 mm.
$\frac{a}{a + f}$	0.594	0.5566	0.339	0.0583
F	41-45	c. 28	11-16	
Sp	8	5	3	
X	138	117	96	
S	1.62 cm.	0.788 cm.	0.17 cm.	0.409 cm.
s x w	143	104.5	68	20.4
P	3.65 mm.	2.882 mm.	2.05 mm.	0.378 mm.
Y	114	73	50	

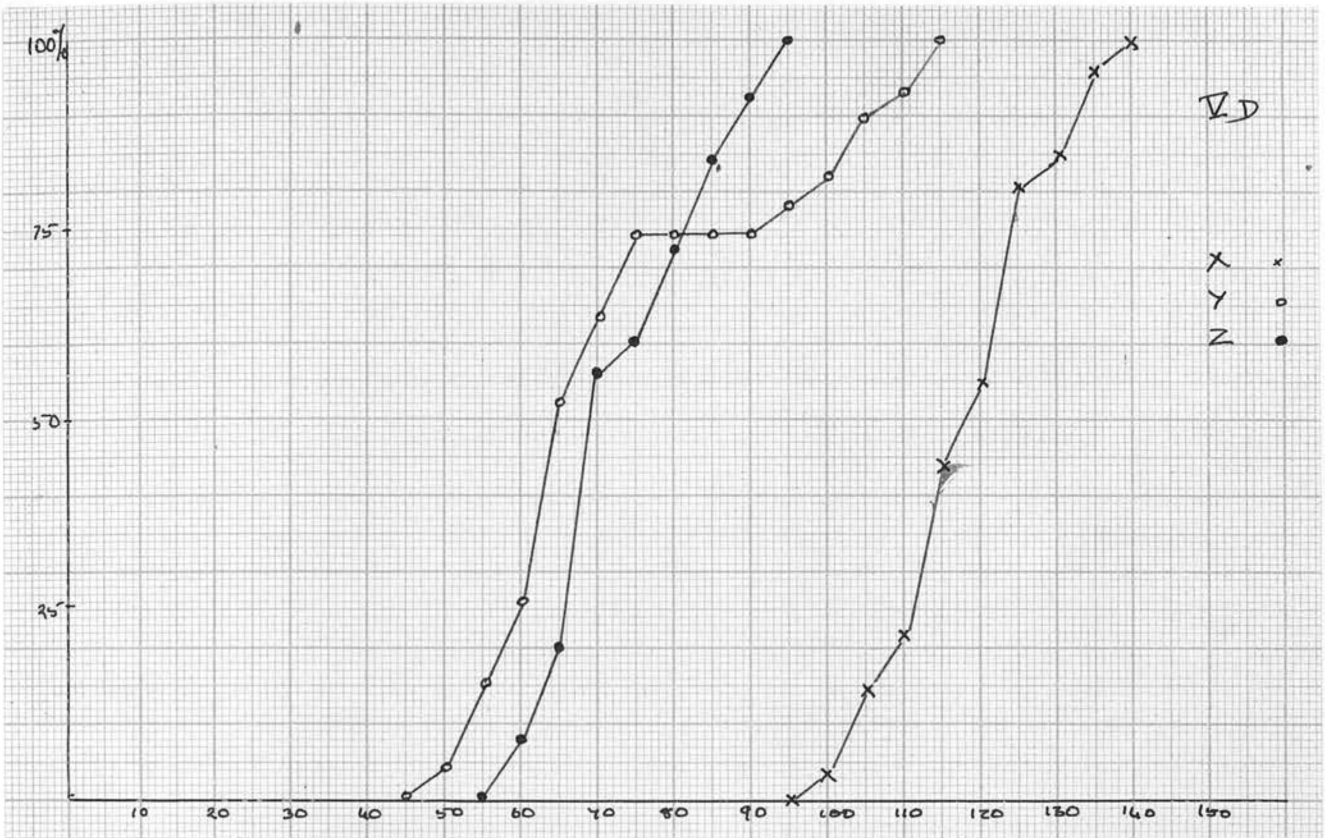
VI

Date : 4/8/55 Grid reference : 27/740448 - 764460

Locality : Drummond Hill, near Kenmore, Perthshire.

Habitat : At sides of track through plantation of mixed Conifers. Growing with <u>Juncus</u> spp., grasses etc.

Character	max.	mean	min.	standard deviation
H	68.0 cm.	42.1 cm.	17.0 cm.	12.4 cm.
L	15.5 cm.	10.28 cm.	5.0 cm.	3.11 cm.
B	0.42 cm.	0.312 cm.	0.19 cm.	0.057 cm.
Z	104	81	48	
s/w	1.66	1.501	1.25	0.087
a + f	1.86 mm.	1.533 mm.	1.12 mm.	0.179 mm.
$\frac{a}{a+f}$	0.645	0.5299	0.437	0.0473
F	61-65	c. 33	11-15	
Sp	8	4-5	2	
X	126	110	94	
S	2.24 cm.	1.095 cm.	0.17 cm.	0.574 cm.
s x w	144	110.1	82	12.5
P	3.95 mm.	3.06 mm.	2.55 mm.	0.335
Y	113	70	51	



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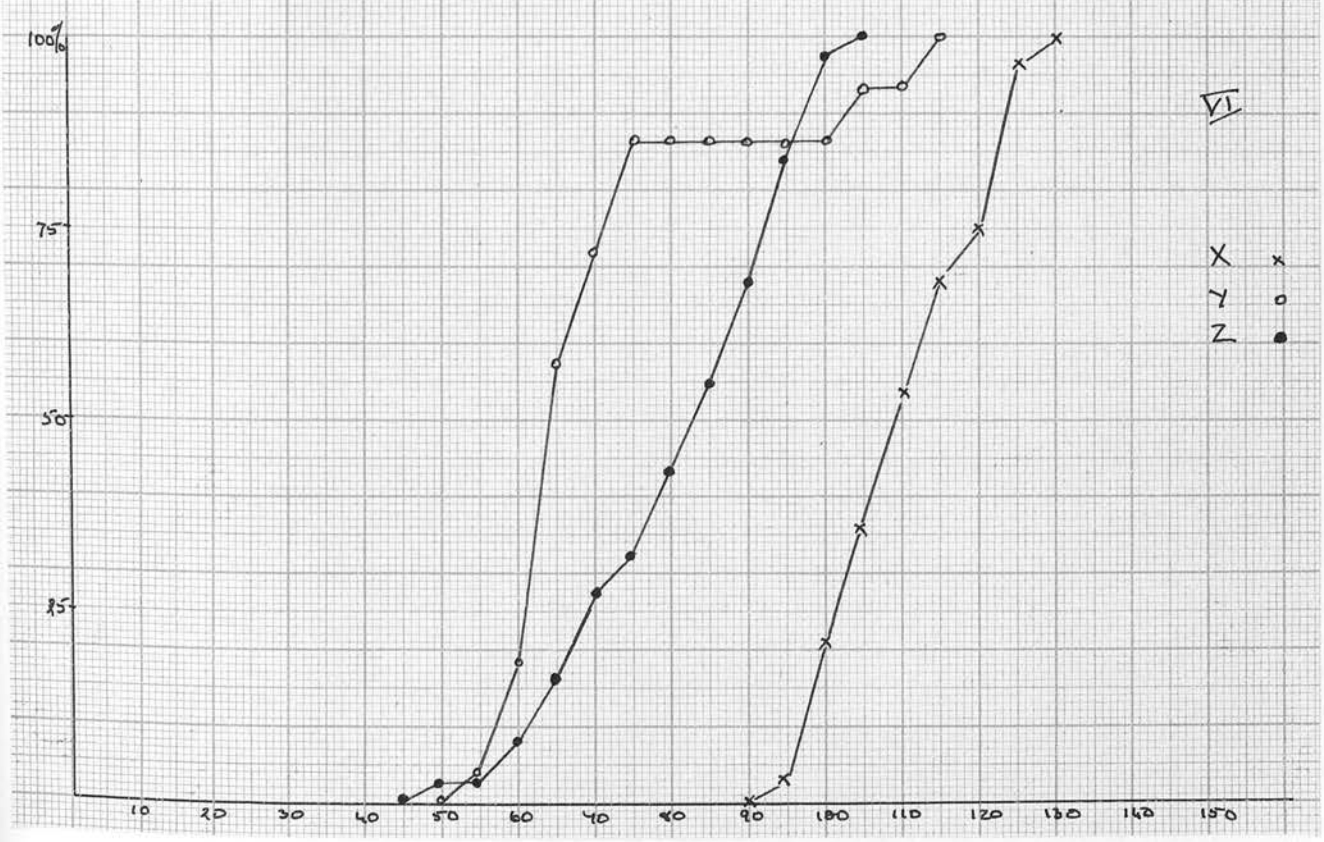

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Fig. 64 a and b

VII A

Date : 5/8/55 Altitude : 700 ft.

Locality : Lawers, Perthshire. Grid Reference : 27/677398

Habitat : Damp pasture on slight south slope. Juncus acutiflorus locally dominant; Holcus lanatus, Ranunculus flammula, Parnassia palustris, Succisa pratensis and Juncus conglomeratus also present.

Character	max.	mean	min.	standard deviation
H	69.0 cm.	42.3 cm.	17.0 cm.	11.1 cm.
L	16.4 cm.	9.90 cm.	5.8 cm.	2.79 cm.
B	0.48 cm.	0.322 cm.	0.23 cm.	0.067 cm.
Z	111	80	52	
s/w	1.66	1.511	1.37	0.066
a + f	1.82 mm.	1.442 mm.	1.16 mm.	0.188 mm.
$\frac{a}{a + f}$	0.605	0.5134	0.379	0.0538
F	46-50	c. 27	11-16	
Sp	9	4	2	
X	132	109	90	
S	1.13 cm.	0.436 cm.	0.15 cm.	0.311 cm.
s x w	149	121.1	90	15.9
Y	122	93	59	

VII B

Date : 5/8/55 Altitude : 700 ft.

Locality : Lawers. Grid Reference : 27/677398

Habitat : Pasture at top of bank at side of burn, drier than VII A. Festuca rubra dominant; Anthoxanthum odoratum frequent; Holcus lanatus, Nardus stricta, Briza media, Trifolium repens, Plantago lanceolata and Succisa pratensis also present.

Character	max.	mean	min.	standard deviation
H	45.0 cm.	29.5 cm.	17.0 cm.	7.3 cm.
L	12.1 cm.	8.40 cm.	4.6 cm.	1.97 cm.
B	0.38 cm.	0.301 cm.	0.15 cm.	0.058 cm.
Z	90	69	44	
s/w	1.67	1.448	1.22	0.102
a + f	1.96 mm.	1.454 mm.	1.05 mm.	0.186 mm.
$\frac{a}{a + f}$	0.631	0.5075	0.345	0.0603
F	46-50	c. 25	11-16	
Sp	7	4	2	
X	121	103	67	
S	1.23 cm.	0.599 cm.	0.12 cm.	0.324 cm.
s x w	150	122.1	93	14.8
P	3.95 mm.	3.269 mm.	2.75 mm.	0.328 mm.
Y	111	88	64	

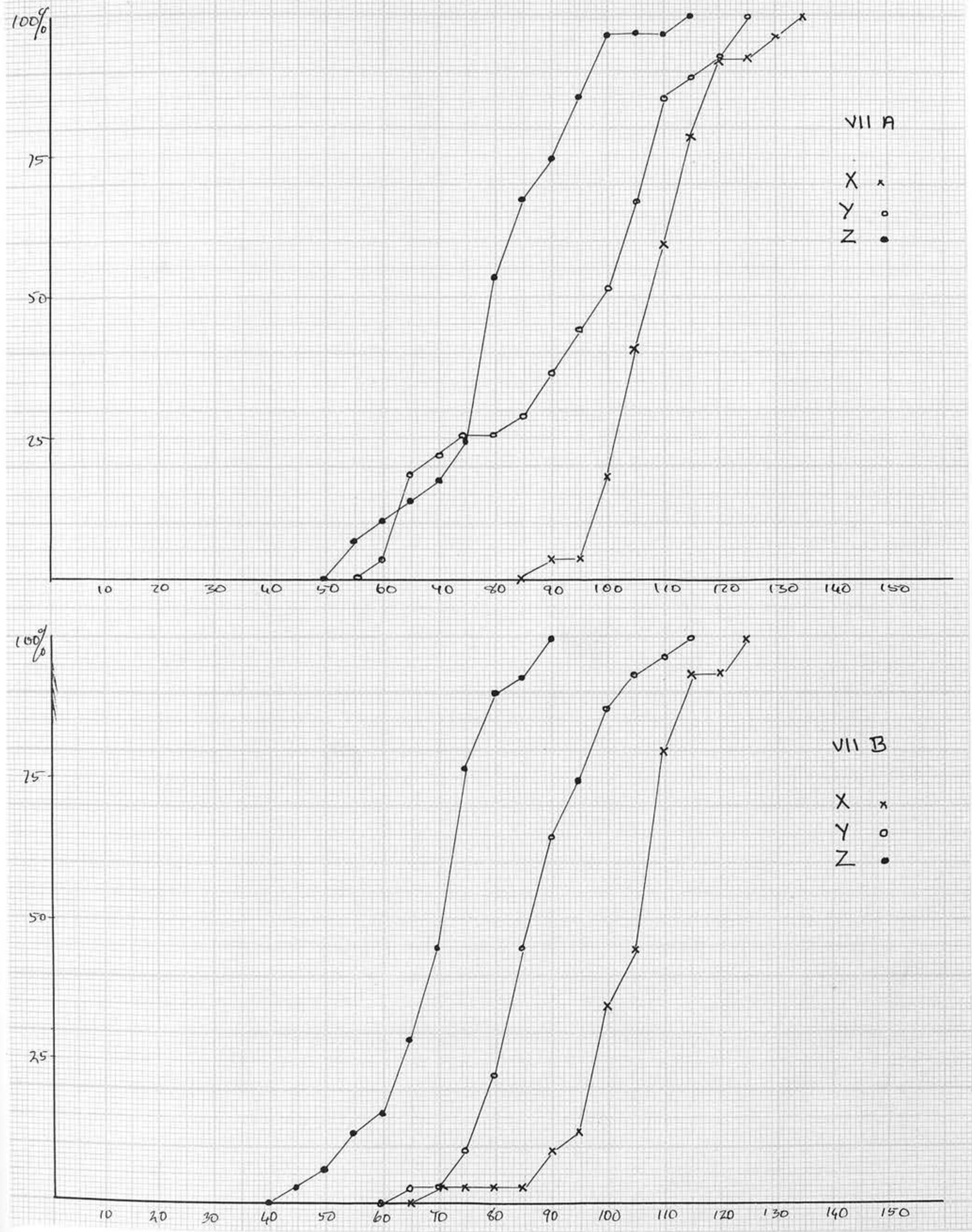

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Fig. 65 a and b

XII A

Date : 29/6/56

Locality : near Carrbridge, Inverness-shire.

Habitat : Bank at edge of river. Nardus stricta abundant; Juncus squarrosus, Potentilla erecta and Galium saxatile frequent.

Character	max.	mean	min.	standard deviation
H	36.0 cm.	27.4 cm.	15.5 cm.	5.4 cm.
L	17.6 cm.	10.36 cm.	5.3 cm.	2.56 cm.
B	0.56 cm.	0.303 cm.	0.21 cm.	0.067 cm.
Z	95	72	48	
s/w	(1.90	1.803	1.75	-) *
a + f	1.77 mm.	1.477 mm.	1.18 mm.	0.148 mm.
$\frac{a}{a+f}$	0.602	0.5184	0.418	0.0496
F	61-65	c.38	21-25	
Sp	8	5	3	
X	144	128	114	
S	1.16 cm.	0.44 cm.	0.15 cm.	0.33 cm.
s x w	(107	97.0	86	-) *
P	4.10 mm.	3.46 mm.	2.60 mm.	0.338 mm.
Y	103	95	84	

* The seeds from most of the plants in this population were not fully ripe, and only a few were available at all; the ratio s/w is abnormally high, and the seed size, s x w, is low.

XII B

Date : 29/6/56

Locality : near Carrbridge.

Habitat : Pasture at edge of river; fairly dry and more or less level. Festuca ovina var. vivipara abundant; Juncus squarrosus, Potentilla erecta, Galium saxatile and Trifolium repens frequent.

Character	max.	mean	min.	standard deviation
H	17.0 cm.	12.5 cm.	6.5 cm.	2.797 cm.
L	9.2 cm.	4.86 cm.	2.5 cm.	1.43 cm.
B	0.31 cm.	0.214 cm.	0.10 cm.	0.053 cm.
Z	57	41	24	
s/w	1.45	1.332	1.18	0.093
a + f	2.17 mm.	1.597 mm.	1.16 mm.	0.221 mm.
$\frac{a}{a + f}$	0.773	0.597	0.458	0.093
F	31-35	c. 18	6-10	
Sp	5	3	2	
X	78	66	48	
S	1.50 cm.	0.687 cm.	0.17 cm.	0.348 cm.
s x w	126	105.7	90	9.4
P	4.05 mm.	3.280 mm.	2.65 mm.	0.341 mm.
Y	110	80	71	

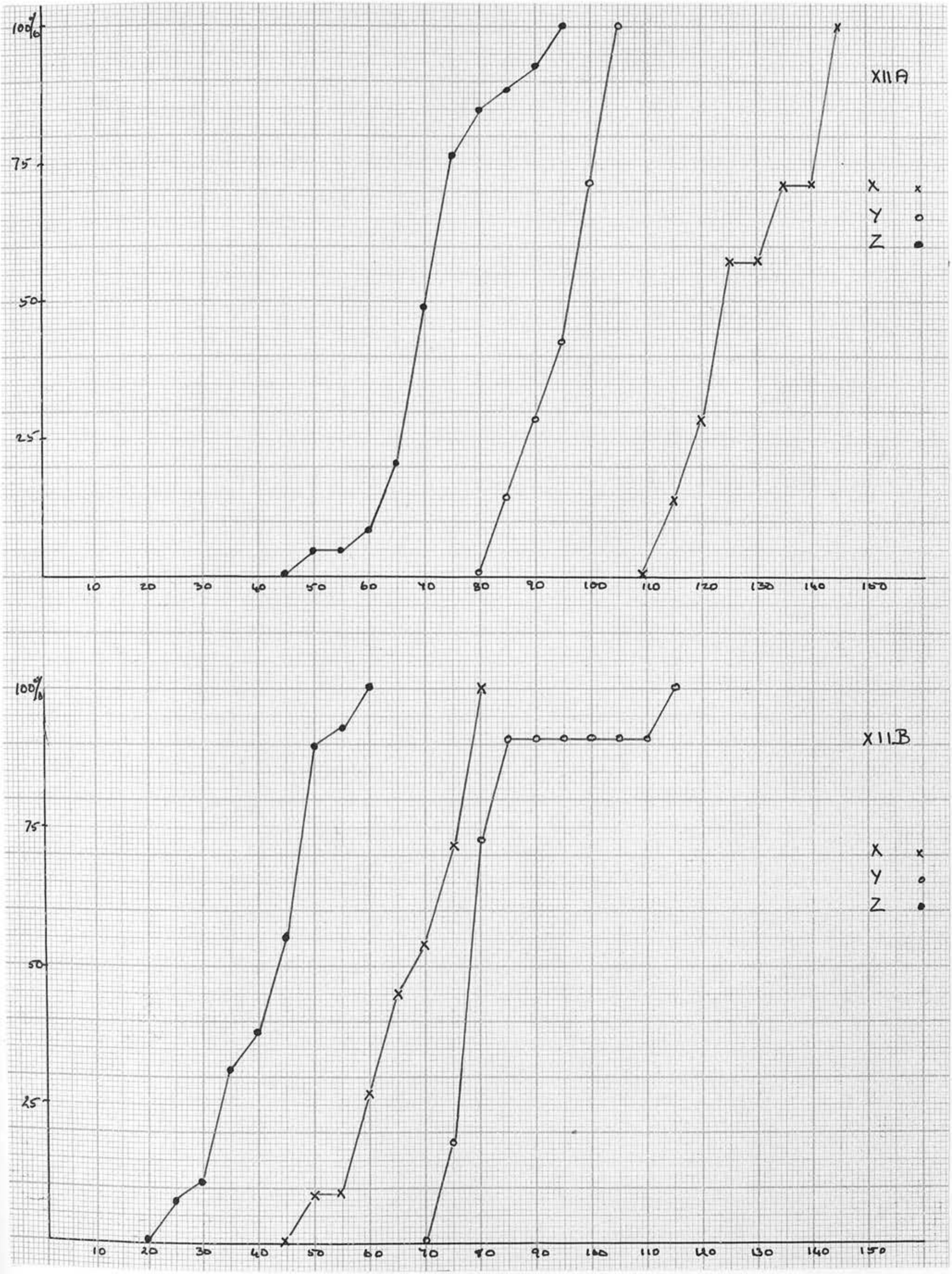
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Fig. 66 a and b

XIII A

Date : 10/7/56

Locality : Ahosnich, Ardnamurchan.

Habitat : Bog, level and more or less drained in places by ditches. Growing with <u>Juncus effusus</u>, <u>Galium palustre</u>, <u>Ranunculus flammula</u>, <u>Filipendula ulmaria</u> and <u>Myrica gale</u>.

Character	max.	mean	min.	standard deviation
H	58.5 cm.	40.1 cm.	28.0 cm.	7.2 cm.
L	20.5 cm.	11.09 cm.	5.4 cm.	2.89 cm.
B	0.44 cm.	0.340 cm.	0.28 cm.	0.048 cm.
Z	107	83	63	
s/w	1.70	1.558	1.37	0.103
a + f	1.79 mm.	1.493 mm.	1.24 mm.	0.147 mm.
$\frac{a}{a + f}$	0.636	0.5033	0.351	0.0672
F	86-90-	c. 40	16-20	
Sp	9	5	3	
X	148	117	90	
S	2.08 cm.	0.572 cm.	0.16 cm.	0.508 cm.
$s \times w^{\frac{2}{3}}$	143	121.4	96	16.9
P	4.05 mm.	3.336 mm.	2.75 mm.	0.308 mm.
Y	119	92	46	

XIII B

Date : 12/7/56

Locality : Grigadale, Ardnamurchan.

Habitat : Bog in a small valley near the shore. Ranunculus flammula abundant; Juncus effusus, Cynosurus cristatus, Carex echinata, Trichophorum caespitosum and Hydrocotyle vulgaris frequent.

Character	max.	mean	min.	standard deviation
H	63.0 cm.	37.8 cm.	17.0 cm.	11.8 cm.
L	22.9 cm.	13.90 cm.	6.3 cm.	4.16 cm.
B	0.36 cm.	0.281 cm.	0.21 cm.	0.049 cm.
Z	109	81	55	
s/w	1.63	1.545	1.42	0.072
a + f	1.82 mm.	1.491 mm.	1.16 mm.	0.189 mm.
$\frac{a}{a + f}$	0.621	0.4856	0.395	0.0486
F	41-45	c. 31	16-20	
Sp	7	4-5	3	
X	124	113	97	
S	1.31 cm.	0.503 cm.	0.13 cm.	0.379 cm.
s x w	156	120.5	95	17.5
P	4.40 mm.	3.483 mm.	2.60 mm.	0.403 mm.
Y	123	96	66	

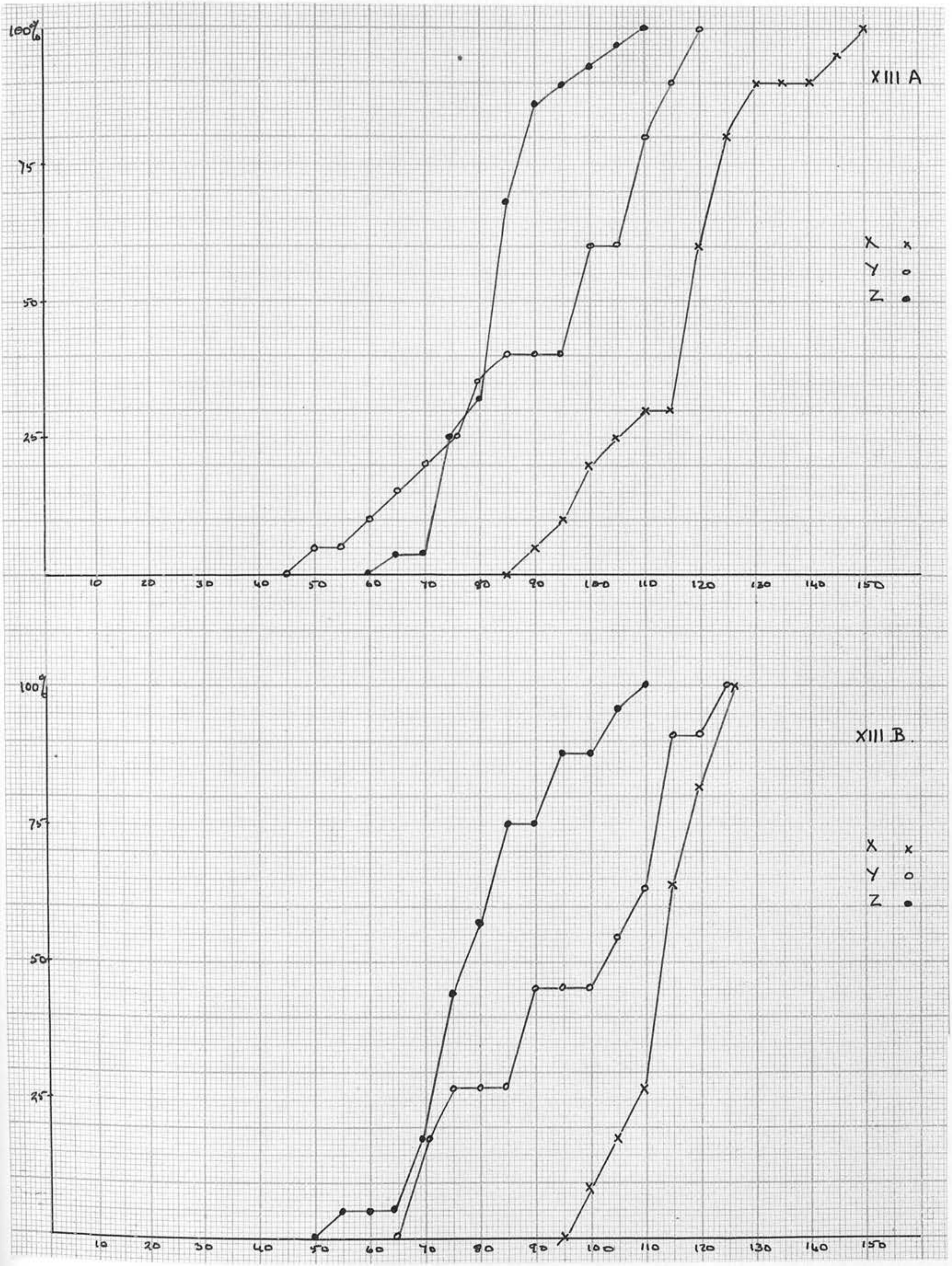

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Fig. 67 a and b

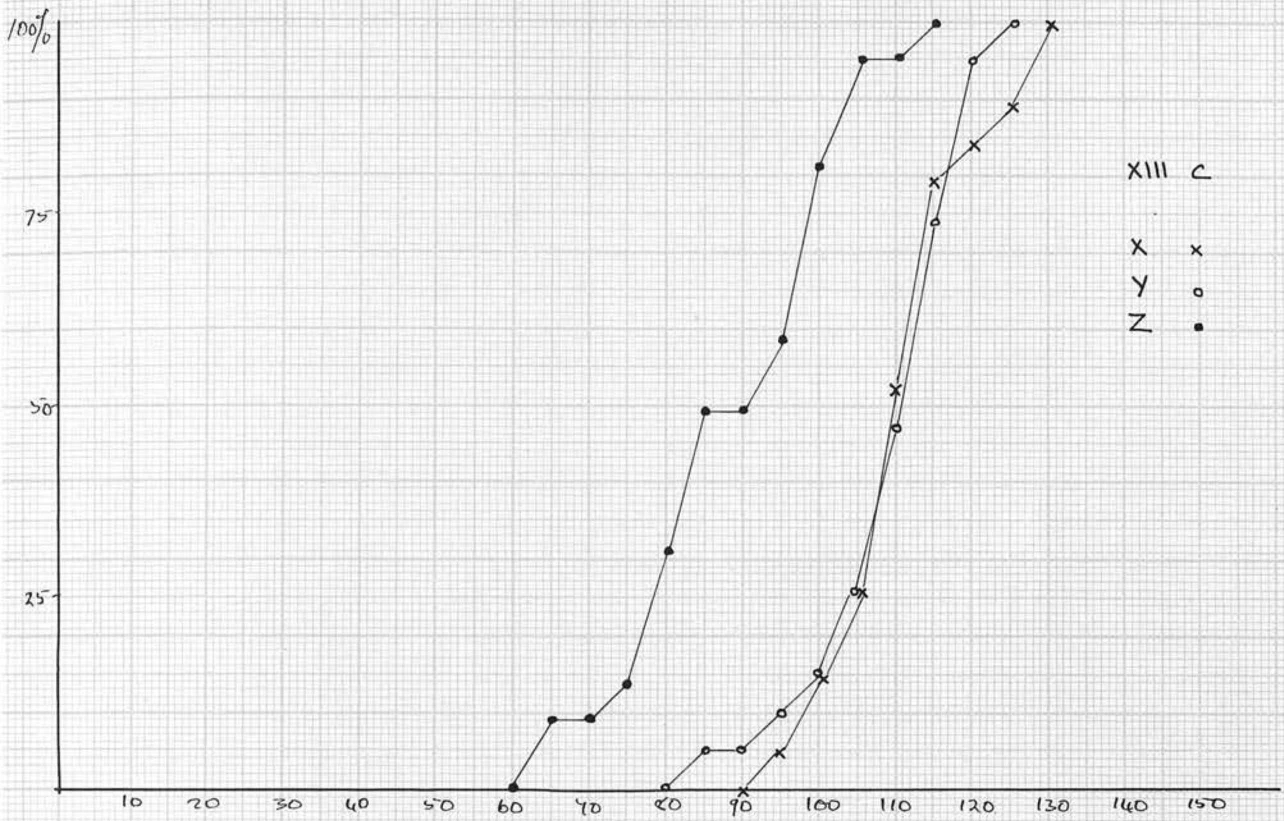
XIII C

Date : 12/7/56

Locality : Ahosnich, Ardnamurchan.

Habitat : Heath and bog in small valley. Growing with *Juncus conglomeratus*, *Festuca rubra*, *Calluna vulgaris*, *Myrica gale* and *Betula pubescens*.

Character	max.	mean	min.	standard deviation
H	60.0 cm.	43.1 cm.	26.0 cm.	8.5 cm.
L	23.1 cm.	12.62 cm.	5.7 cm.	3.74 cm.
B	0.62 cm.	0.369 cm.	0.20 cm.	0.997 cm.
Z	112	88	61	
s/w	1.60	1.462	1.38	0.058
a + f	1.84 mm.	1.545 mm.	1.22 mm.	0.159 mm.
$\frac{a}{a+f}$	0.658	0.4931	0.333	0.0722
F	76-80	c. 40	21-25	
Sp	9	5-6	4	
X	129	111	92	
S	1.21 cm.	0.407 cm.	0.19 cm.	0.248 cm.
s x w	159	137.4	105	12.1
P	4.00 mm.	3.614 mm.	3.15 mm.	0.252 mm.
Y	122	109	81	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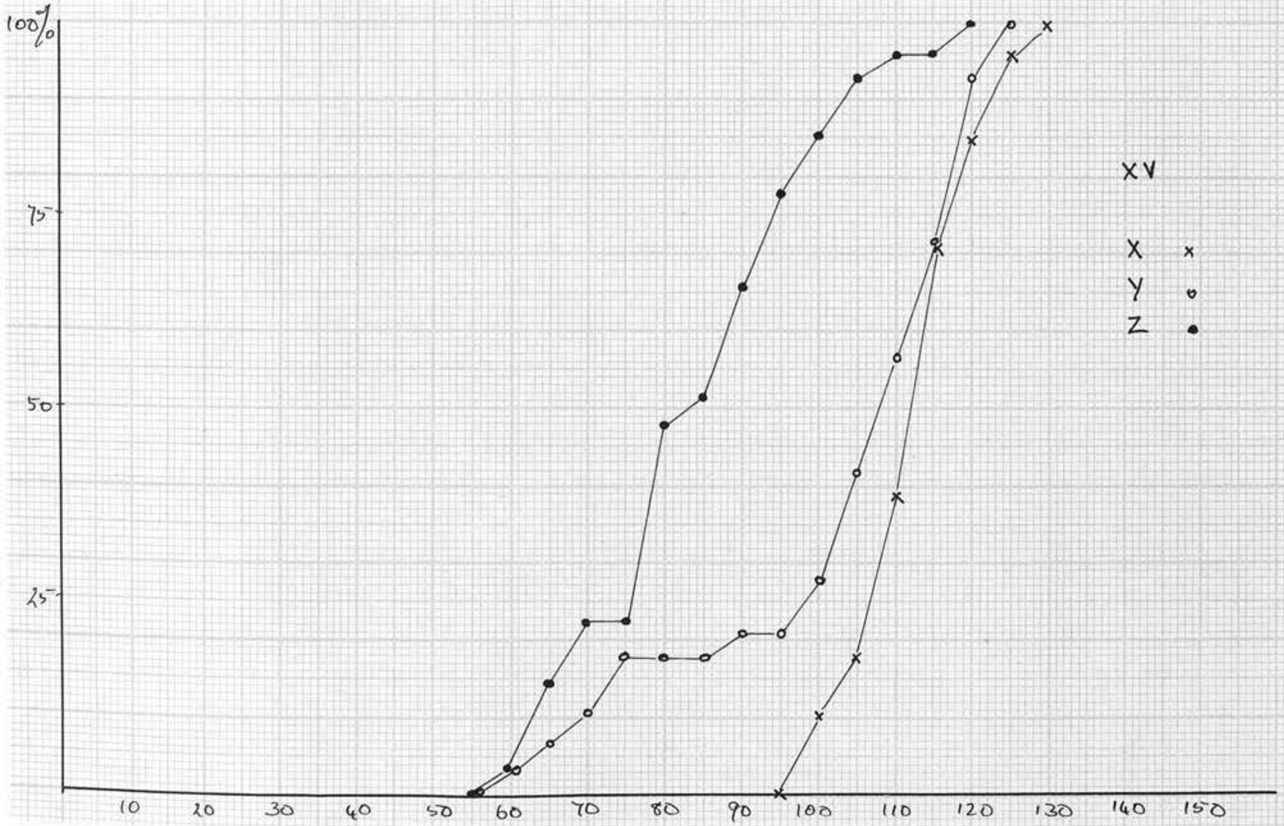
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Fig. 68 a and b

XIV A

Date : 30/7/56

Locality : Plockton, Ross-shire.

Habitat : Wood at edge of path near sea; damp in places.

Deschampsia flexuosa abundant, Juncus effusus locally abundant; Agrostis tenuis, Holcus lanatus, Anthoxanthum odoratum and Pteridium aquilinum frequent.

Character	max.	mean	min.	standard deviation
H	43.0 cm.	31.9 cm.	19.0 cm.	8.6 cm.
L	15.1 cm.	9.1 8 cm.	5.2 cm.	2.27 cm.
B	0.39 cm.	0.289 cm.	0.16 cm.	0.052 cm.
Z	90	71	45	
s/w	1.69	1.474	1.16	0.104
a + f	2.00 mm.	1.521 mm.	1.16 mm.	0.203 mm.
$\frac{a}{a + f}$	0.629	0.5114	0.406	0.0596
F	51-55	c. 33	11-15	
Sp	7	5	2	
X	130	107	69	
S	1.27 cm.	0.651 cm.	0.15 cm.	0.384 cm.
s x w	151	120.5	95	17.5
P	3.95 mm.	3.104 mm.	2.60 mm.	0.363 mm.
Y	119	87	57	

XIV B

Date : 2/8/56

Locality : Plockton, Ross-shire.

Habitat : Roadside at edge of felled wood. Agrostis tenuis abundant; Digitalis purpurea, Veronica officinalis and Ranunculus repens frequent.

Character	max.	mean	min.	standard deviation
H	62.0 cm.	39.1 cm.	17.5 cm.	10.0 cm.
L	18.5 cm.	12.21 cm.	5.6 cm.	3.35 cm.
B	0.45 cm.	0.314 cm.	0.19 cm.	0.068 cm.
Z	110	83	60	
s/w	1.63	1.469	1.25	0.074
a + f	1.82 mm.	1.416 mm.	1.10 mm.	0.163 mm
$\frac{a}{a+f}$	0.637	0.5166	0.373	0.0602
F	76-80	c. 38	21-25	
Sp	9	5	3	
X	134	113	91	
S	1.84 cm.	0.789 cm.	0.16 cm.	0.488 cm.
s x w	172	115.2	81	18.7
P	3.90 mm.	3.096 mm.	2.60 mm.	0.317 mm.
Y	116	81	49	

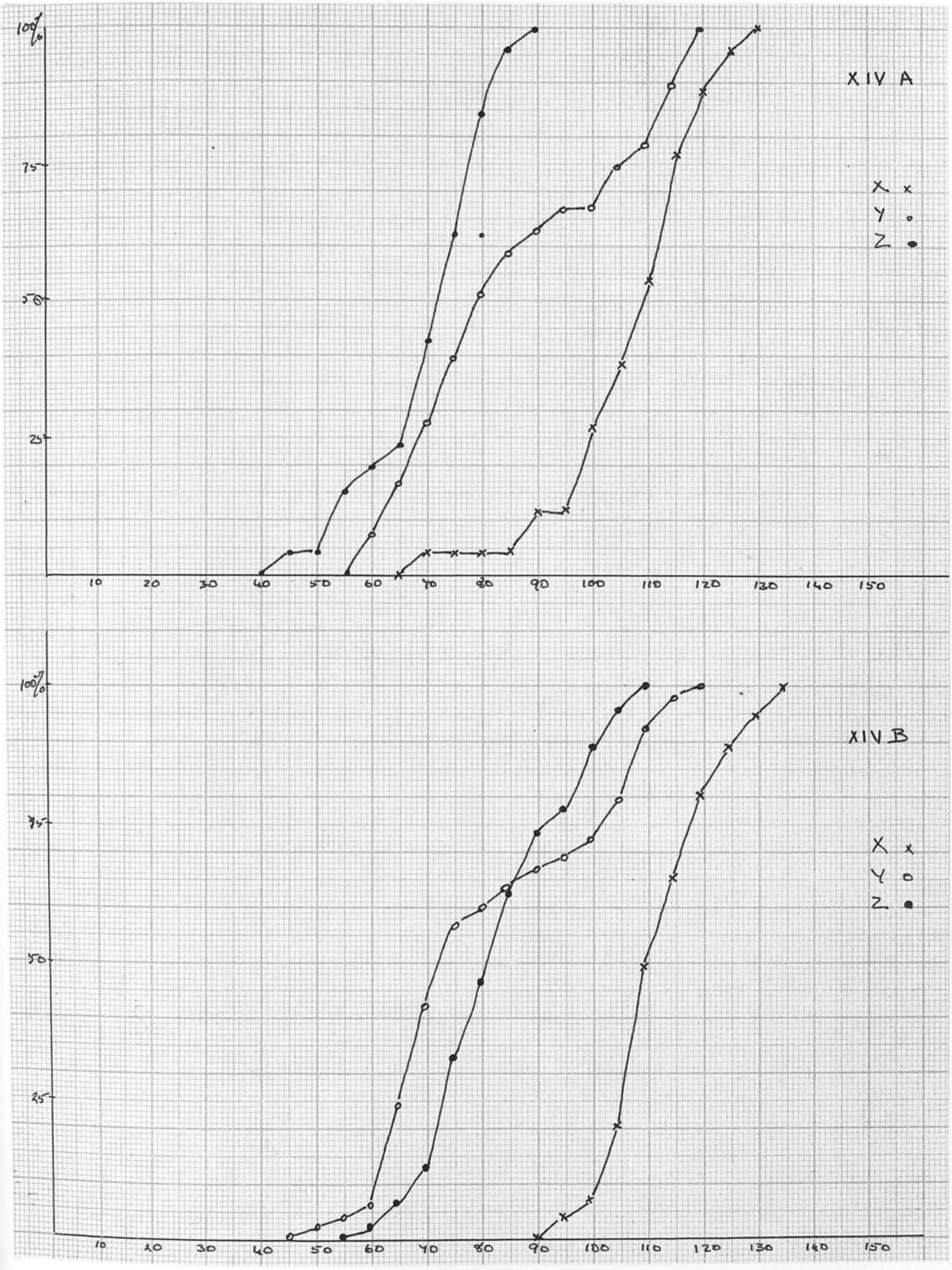

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Fig. 69 a and B

XIV C

Date : 2/8/56

Locality : Plockton.

Habitat : Open patch in wood, and in felled part of wood; rather damp; at a lower level than XIV B. Agrostis tenuis abundant; Juncus effusus, Holcus lanatus and Ranunculus flammula frequent.

Character	max.	mean	min.	standard deviation
H	55.0 cm.	37.2 cm.	28.0 cm.	6.9 cm.
L	16.9 cm.	10.32 cm.	6.6 cm.	2.32 cm.
B	0.42 cm.	0.304 cm.	0.18 cm.	0.064 cm.
Z	95	78	61	
s/w	1.71	1.471	1.35	0.074
a + f	1.86 mm.	1.477 mm.	1.06 mm.	0.207 mm.
$\frac{a}{a+f}$	0.662	0.5151	0.375	0.0651
F	76-80	c. 42	16-20	
Sp	8	5-6	3	
X	139	112	91	
S	1.56 cm.	0.673 cm.	0.16 cm.	0.347 cm.
s x w	169	118.5	84	21.3
P	3.85 mm.	3.145 mm.	2.60 mm.	0.327 mm.
Y	127	84	59	

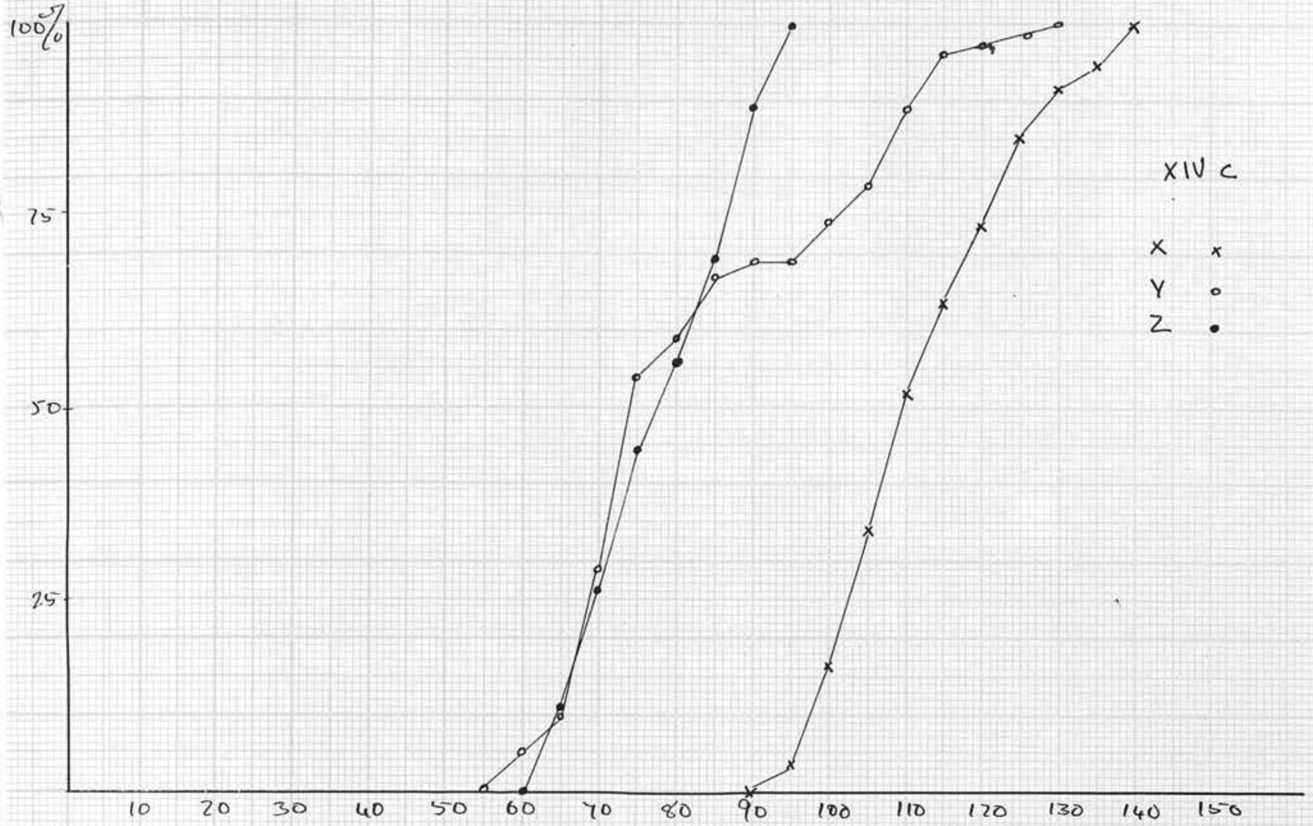
XIV D

Date : 2/8/56

Locality : Plockton.

Habitat : Wood at foot of slope below XIV C, at top of cliff above path (XIV A); Deschampsia flexuosa abundant; Holcus mollis frequent, also Potentilla erecta, Carex panicea, Juncus effusus and Lysimachia nemorum.

Character	max.	mean.	min.	standard deviation
H	61.0 cm.	43.6 cm.	28.0 cm.	9.5 cm.
L	16.9 cm.	11.07 cm.	6.1 cm.	3.17 cm.
B	0.50 cm.	0.332 cm.	0.23 cm.	0.069 cm.
Z	105	84	63	
s/w	1.64	1.511	1.40	0.058
a + f	2.15 mm.	1.483 mm.	1.14 mm.	0.437 mm.
$\frac{a}{a+f}$	0.592	0.4777	0.367	0.061
F	71-75	c. 35	16-20	
Sp	10	5	3	
X	146	115	89	
S	1.59 cm.	0.500 cm.	0.14 cm.	0.455 cm.
s x w	172	132.9	93	22.04
P	4.00 mm.	3.309 mm.	2.50 mm.	0.406 mm.
Y	129	98	58	



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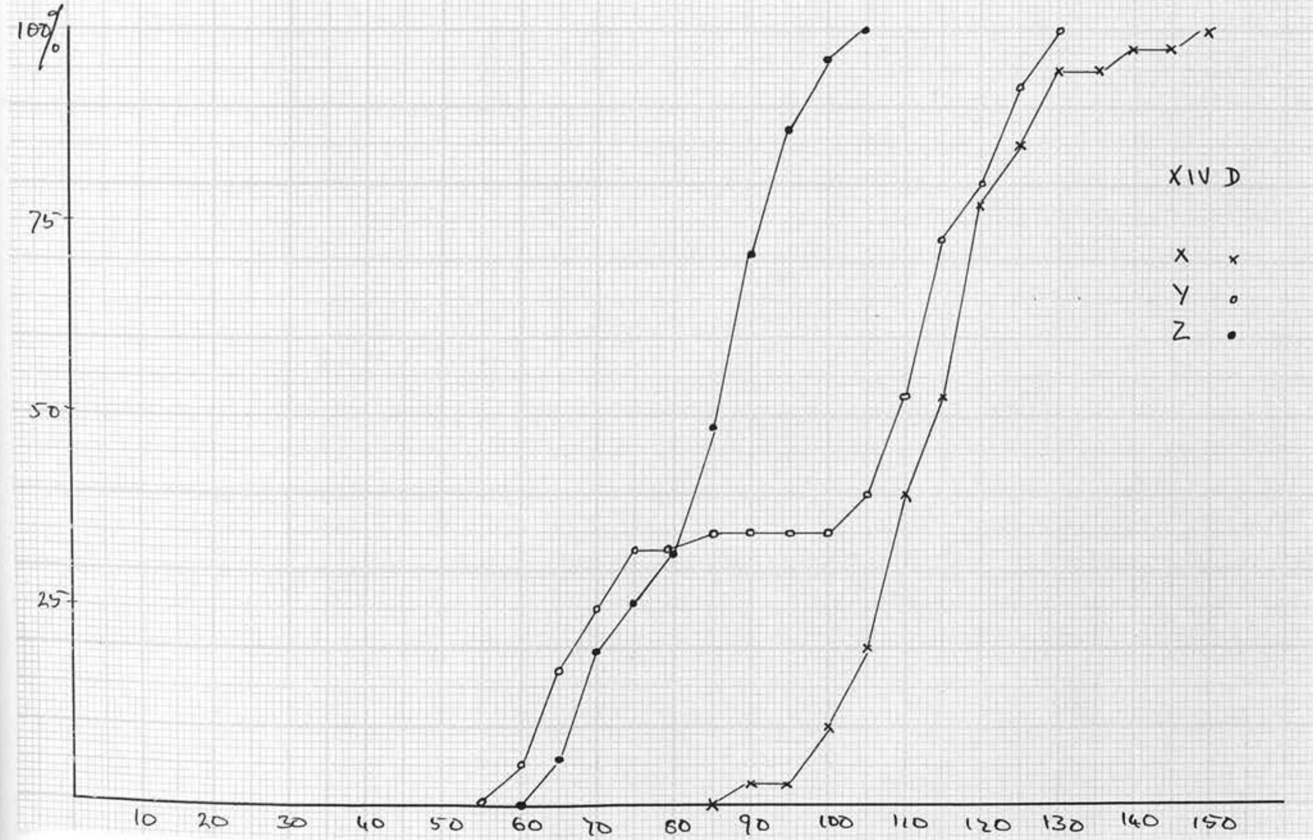

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Fig. 70 a and b

XV

Date : 31/7/56

Locality : Loch Long, Ross-shire; near Killillan.

Habitat : Moor, facing south, with a slight slope. Agrostis tenuis abundant; Calluna vūlgaris, Potentilla erecta and Anthoxanthum odoratum frequent.

Character	max.	mean	min.	standard deviation
H	71.0 cm.	42.7 cm.	23.0 cm.	10.99 cm.
L	20.3 cm.	11.56 cm.	4.9 cm.	3.56 cm.
B	0.42 cm.	0.318 cm.	0.19 cm.	0.069 cm.
Z	117	89	56	
s/w	1.64	1.519	1.37	0.065
a + f	2.00 mm.	1.517 mm.	1.20 mm.	0.0594
$\frac{a}{a+f}$	0.602	0.4950	0.333	0.0594
F	56-60	c. 34	21-25	
Sp	7	5	4	
X	127	111	97	
S	1.39 cm.	0.416 cm.	0.12 cm.	0.360 cm.
s x w	172	133.9	94	19.8
P	3.95 mm.	3.368 mm.	2.60 mm.	0.351 mm.
Y	125	103	58	

XVI

Date : 1/8/56

Locality : Strome, Ross-shire.

Habitat : At edge of track in conifer plantation; high proportion of bare ground.

Character	max.	mean	min.	standard deviation
H	45.5 cm.	29.5 cm.	13.5 cm.	7.3 cm.
L	11.6 cm.	7.35 cm.	4.1 cm.	1.89 cm.
B	0.41 cm.	0.309 cm.	0.17 cm.	0.039 cm.
Z	87	67	41	
s/w	1.59	1.455	1.35	0.066
a + f	1.90 mm.	1.518 mm.	1.24 mm.	0.237 mm.
$\frac{a}{a + f}$	0.623	0.517	0.364	0.0554
F	46-50	c. 28	11-15	
Sp	7	4	3	
X	119	103	80	
S	1.62 cm.	0.747 cm.	0.16 cm.	0.455 cm.
s x w	151	118.6	83	17.7
P	3.75 mm.	3.227 mm.	1.24 mm.	0.292 mm.
Y	118	85	52	

XVII

Date : 3/8/56

Locality : Near Ben Dorainn, Argyll. Grid Reference : 27/32-33-

Habitat : Pasture at roadside; level, dry. Festuca ovina var, vivipara abundant; Nardus stricta, Agrostis tenuis, Juncus squarrosus and Calluna vulgaris frequent.

Character	max.	mean	min.	standard deviation
H	37.0 cm.	26.6 cm.	17.0 cm.	5.1 cm.
L	10.9 cm.	7.66 cm.	4.8 cm.	1.77 cm.
B	0.41 cm.	0.2 92 cm.	0.17 cm.	0.069 cm.
Z	80	65	45	
s/w	1.56	1.418	1.13	0.100
a + f	1.94 mm.	1.486 mm.	1.08 mm.	0.212 mm.
$\frac{a}{a+f}$	0.667	0.5028	0.344	0.0813
F	41-45	c. 23	11-15	
Sp	6	3	2	
X	122	99	71	
S	1.38 cm.	0.464 cm.	0.12 cm.	0.392 cm.
s x w	140	115.4	86	14.0
P	3.65 mm.	3.09 mm.	2.50 mm.	0.282 mm.
Y	110	89	59	

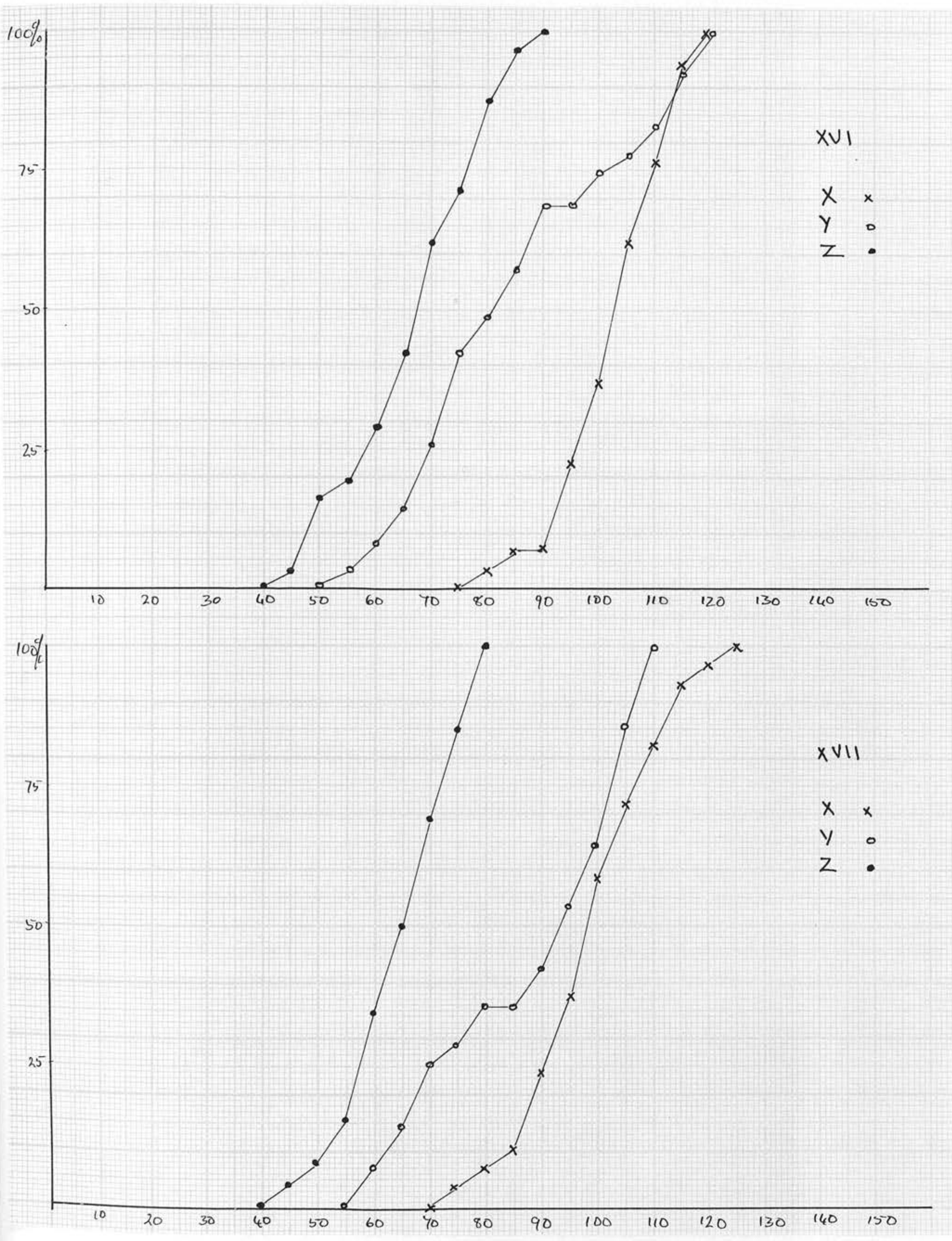

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Fig. 71 a and b

XVIII A

Date : 15/6/57

Locality : Woodwalton Fen, near Huntingdon.

Habitat : Side of path through fen; level and dry (? dry only in summer). Growing with Phragmites communis, Agrostis stolonifera, Galium palustre and Epilobium palustre. Luzula locally abundant, but only in an area about 2 x 3 metres.

Character	max.	mean	min.	standard deviation
H	28.0 cm.	17.5 cm.	9.0 cm.	5.5 cm.
L	13.9 cm.	9.76 cm.	5.1 cm.	2.36 cm.
B	0.34 cm.	0.247 cm.	0.15 cm.	0.052 cm.
Z	75	61	38	
s/w	1.83	1.652	1.41	0.093
a + f	1.62 mm.	1.099 mm.	0.84 mm.	0.271 mm.
$\frac{a}{a+f}$	0.574	0.4816	0.408	0.0531
F	96-100	c. 65	26-30	
Sp	17	c. 8	5	
X	177	149	110	
S	1.41 cm.	0.90 cm.	0.18 cm.	0.329 cm.
s x w	117	60.0	31	21.2
P	3.10 mm.	1.937 mm.	1.40 mm.	0.58 mm.
Y	99	40	19	

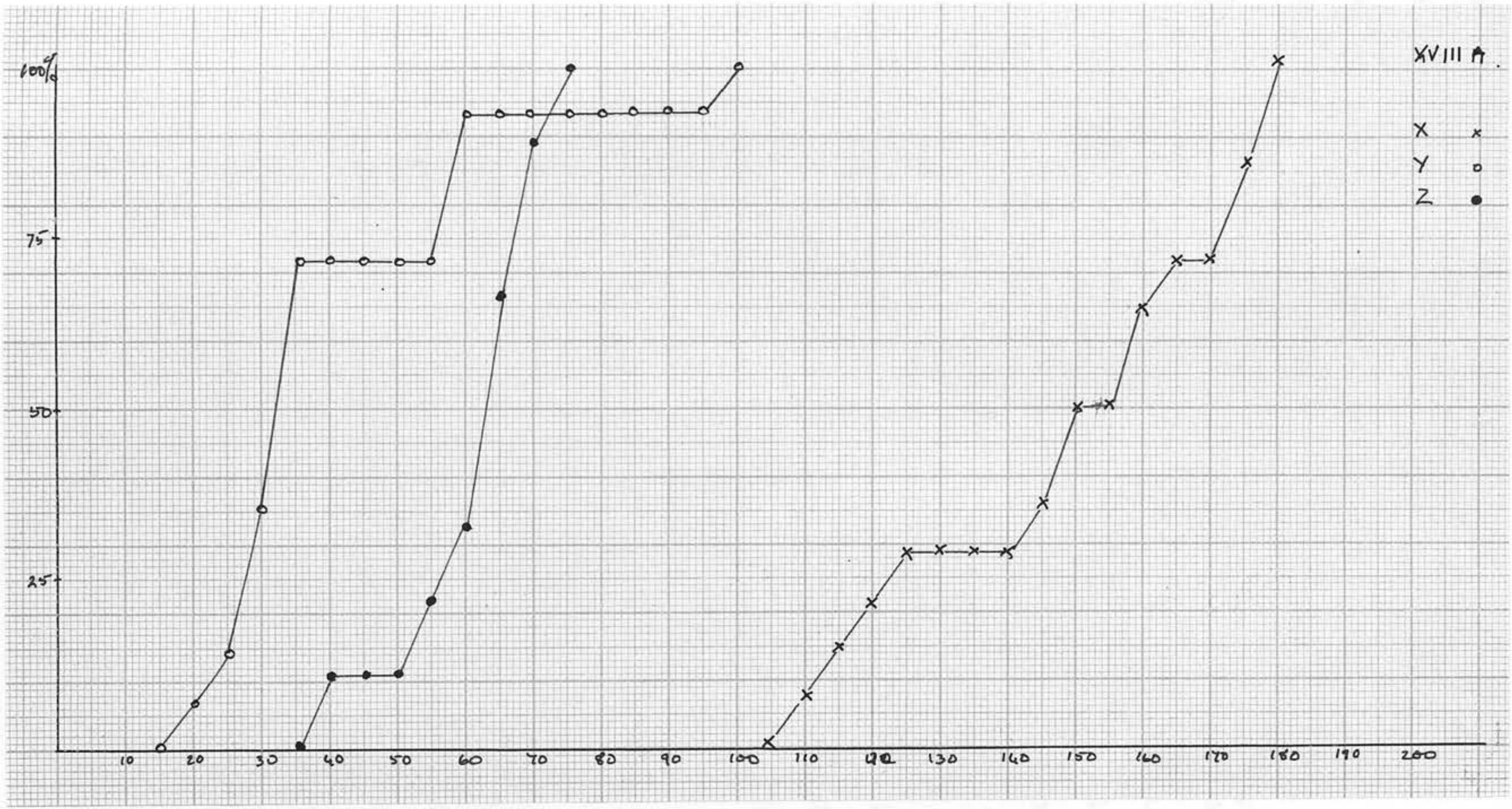
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Fig. 72 a

XVIII B

Date : 15/6/57

Locality : Holme Fen, Huntingdonshire.

Habitat : At edges of path through Birch wood.

Character	max.	mean	min.	standard deviation
H	54.0 cm.	22.1 cm.	13.0 cm.	13.1 cm.
L	18.6 cm.	10.5 cm.	5.0 cm.	4.06 cm.
B	0.36 cm.	0.255 cm.	0.14 cm.	0.066 cm.
Z	99	65	44	
s/w	1.73	1.509	1.29	0.123
a + f	1.84 mm.	1.357 mm.	0.89 mm.	0.087 mm.
$\frac{a}{a + f}$	0.662	0.5577	0.458	0.0626
F	76-80	c. 46	21-25	
Sp	12	6	3	
X	156	120	92	
S	1.83 cm.	0.933 cm.	0.27 cm.	0.353 cm.
s x w	125	78.5	42	22.3
P	3.10 mm.	2.543 mm.	1.50 mm.	0.556 mm.
Y	95	53	23	

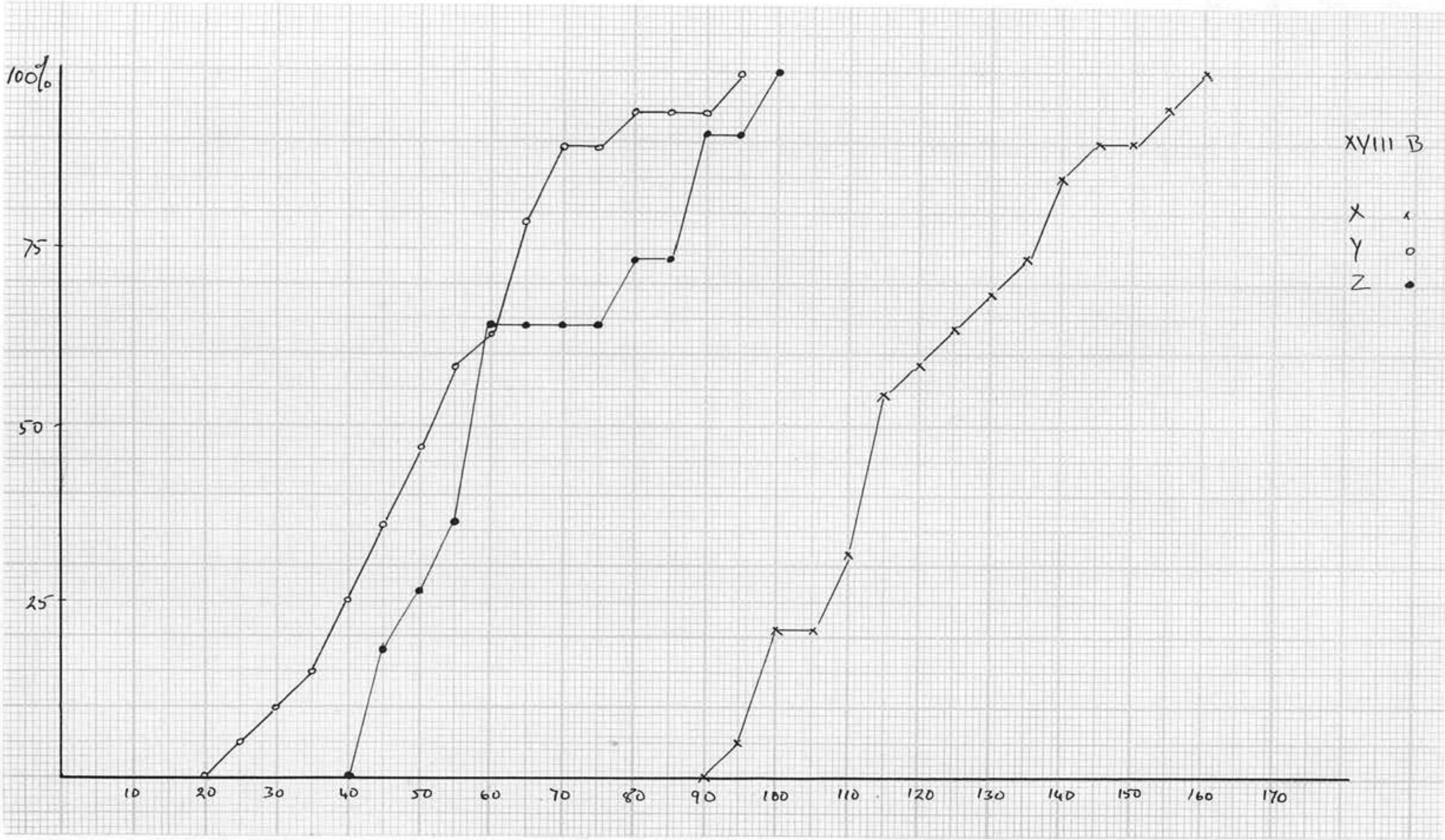

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Fig. 72 b

XIX

Date : 16/6/57

Locality : Leith Hill, Surrey.

Habitat : Edges of path in mixed woodland, with Pinus and Betula; appeared not to extend far into wood. Growing with Deschampsia flexuosa, Galium saxatile, Pteridium aquilinum and Anthoxanthum odoratum.

Character	max.	mean	min.	standard deviation
H	54.5 cm.	33.2 cm.	17.5 cm.	9.5 cm.
L	21.1 cm.	14.60 cm.	6.7 cm.	3.95 cm.
B	0.49 cm.	0.329 cm.	0.15 cm.	0.084 cm.
Z	110	82	52	
s/w	1.83	1.655	1.45	0.132
a + f	1.79 mm.	1.586 mm.	1.22 mm.	0.126 mm.
$\frac{a}{a + f}$	0.627	0.5239	0.380	0.0587
F	56-60	c. 38	11-15	
Sp	7	4-5	2	
X	132	113	89	
S	2.56 cm.	0.603 cm.	0.16 cm.	0.526 cm.
s x w	113	87.9	76	11.1
P	3.65 mm.	3.129 mm.	2.40 mm.	0.268 mm.
Y	100	77	47	

XX A

Date : 14/7/57

Locality : Burn of Cannie, Aberdeenshire.

Habitat : Open heath, with some colonisation by _Betula_; fairly dry. Growing with _Juncus squarrosus_, _Agrostis canina_, _Deschampsia flexuosa_, _Galium saxatile_, _Calluna vulgaris_ and _Potentilla erecta_.

Character	max.	mean	min.	standard deviation
H	45.0 cm.	31.9 cm.	21.0 cm.	6.0 cm.
L	19.4 cm.	10.67 cm.	5.6 cm.	2.84 cm.
B	0.43 cm.	0.300 cm.	0.18 cm.	0.065 cm.
Z	99	74	53	
s/w	1.68	1.511	1.42	0.069
a + f	1.84 mm.	1.408 mm.	1.05 mm.	0.165 mm.
$\frac{a}{a+f}$	0.634	0.5149	0.382	0.0535
F	61-65	c. 35	11-15	
Sp	6	4-5	3	
X	130	111	91	
S	1.29 cm.	0.468 cm.	0.16 cm.	0.296 cm.
s x w	147	107.0	70	17.3
P	3.80 mm.	3.130 mm.	2.25 mm.	0.359 mm.
Y	112	86	53	

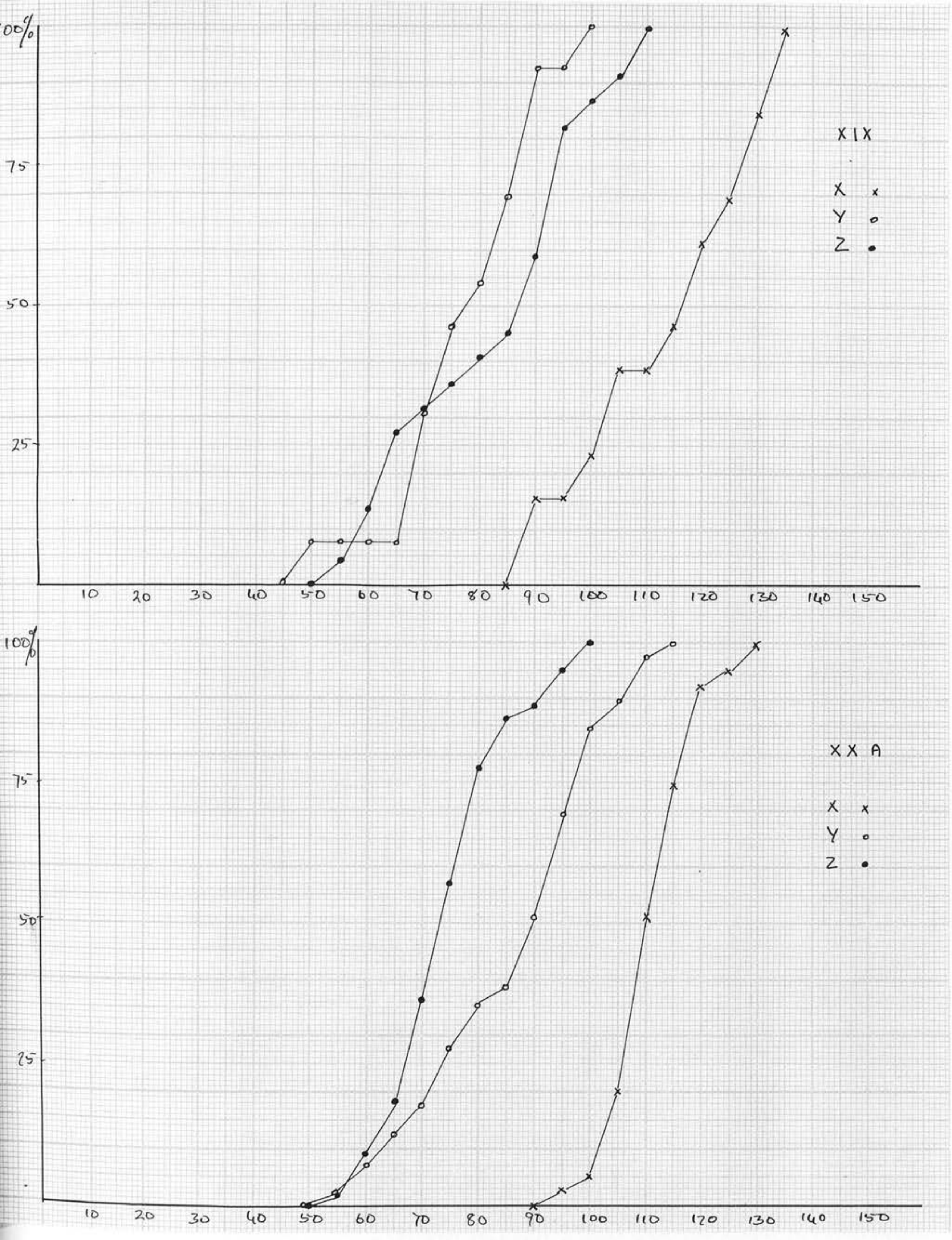
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Fig. 73 a and b

XX B

Date : 1 4/7/57

Locality : Dess, Aberdeenshire. Grid Reference : 38/566003

Habitat : Steep, west-facing bank, formerly wooded. Growing with *Agrostis tenuis* and *Holcus lanatus.*

Char-acter	max.	mean	min.	standard deviation
H	36.5 cm.	28.1 cm.	20.0 cm.	4.1 cm.
L	15.5 cm.	11.68 cm.	8.0 cm.	1.77 cm.
B	0.39 cm.	0.276 cm.	0.21 cm.	0.047 cm.
Z	83	73	61	
s/w	1.65	1.451	1.22	0.098
a + f	1.69 mm.	1.368 mm.	1.14 mm.	0.191 mm.
$\frac{a}{a+f}$	0.662	0.5150	0.350	0.0781
F	66-70	c. 50	26-30	
X	144	119	87	
S	1.54 cm.	1.091 cm.	0.81 cm.	0.219 cm.
s x w	118	81.9	59	16.5
P	3.60 mm.	2.668 mm.	2.15 mm.	0.396 mm.
Y	85	54	32	

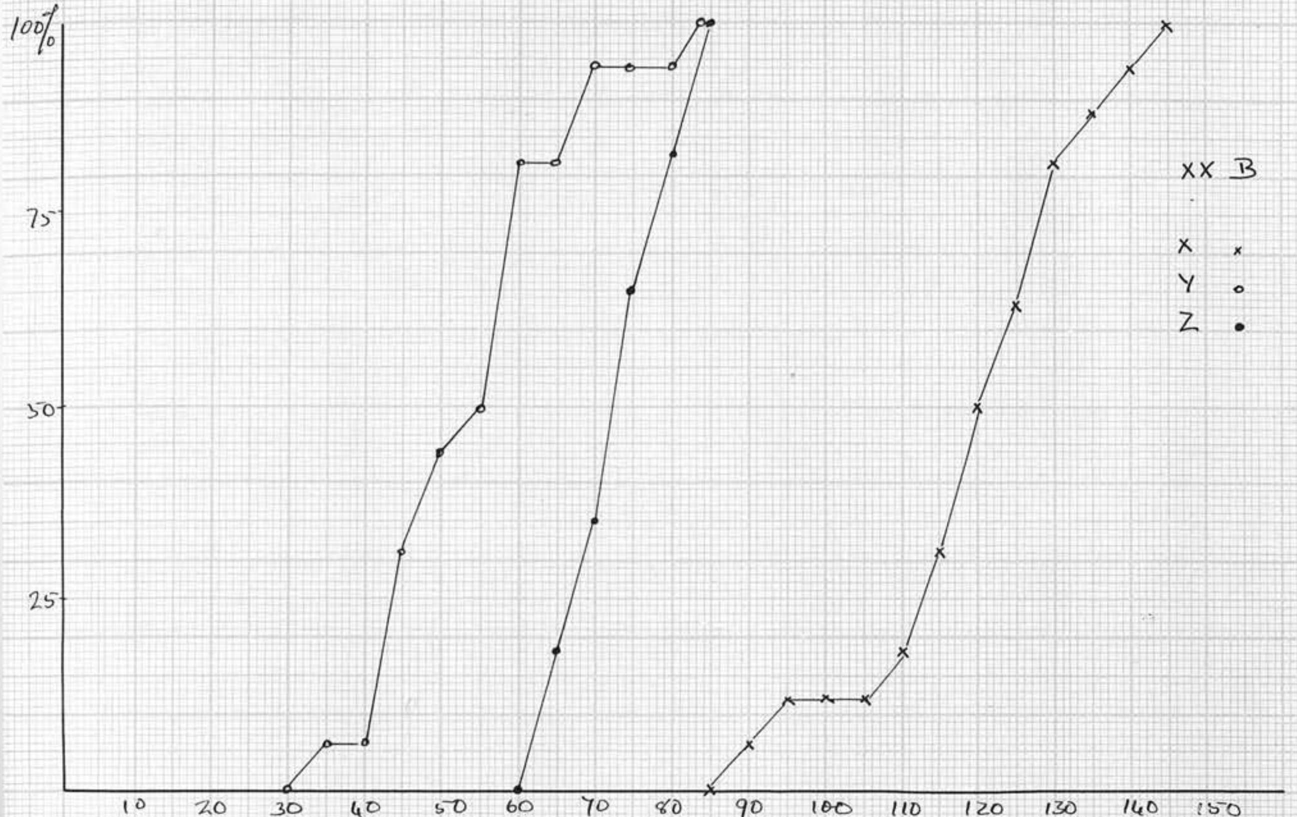
XX C

Date : 14/7/57

Locality : Dess, Aberdeenshire.   Grid Reference : 38/566003

Habitat : Bank at edge of wood; between coniferous palntation on hillside and communitty at edge of river with Alnus and Betula. Juncus spp., Filipendula ulmaria and Valeriana officinalis in ground flora. Very wet in places.

Character	max.	mean	min.	standard deviation
H	74.5 cm.	45.9 cm.	23.5 cm.	13.1 cm.
L	19.9 cm.	12.81 cm.	8.9 cm.	3.39 cm.
B	0.55 cm.	0.396 cm.	0.26 cm.	0.067 cm.
Z	128	93	70	
s/w	1.64	1.515	1.40	0.075
a + f	1.86 mm.	1.501 mm.	1.10 mm.	0.169 mm.
$\frac{a}{a+f}$	0.603	0.5121	0.392	0.0567
F	56-60	c. 41	26-30	
Sp	7	5	4	
X	130	114	100	
S	2.14 cm.	0.398 cm.	0.14 cm.	0.439 cm.
s x w	142	121.1	94	13.9
P	3.75 mm.	3.253 mm.	2.60 mm.	0.262 mm.
Y	110	97	50	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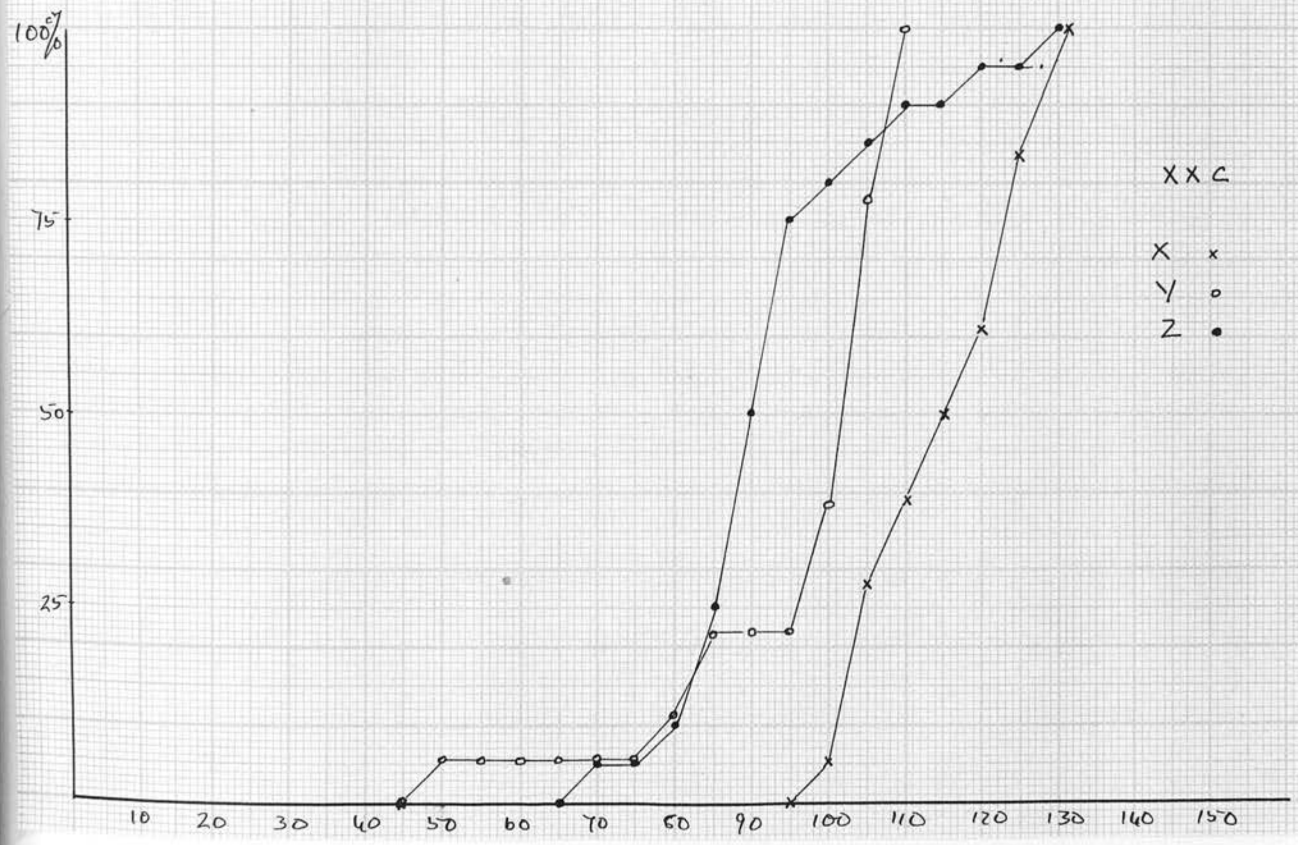
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Fig. 74 a and b

XXI

Date : 15/7/57

Locality : Cothill, north of Aberdeen.

Habitat : Dune pasture, rather dry. Growing with *Festuca rubra*, *Holcus lanatus* etc.

Character	max.	mean	min.	standard deviation
H	31.0 cm.	22.9 cm.	13.0 cm.	4.7 cm.
L	14.0 cm.	9.80 cm.	5.40 cm.	2.41 cm.
B	0.35 cm.	0.249 cm.	0.17 cm.	0.044 cm.
Z	76	64	43	
s/w	1.33	1.200	1.07	0.076
a + f	2.39 mm.	1.932 mm.	1.46 mm.	0.243 mm.
$\frac{a}{a+f}$	0.816	0.7074	0.610	0.0523
F	36–40	c. 23	11–15	
Sp	5	3–4	2	
X	76	62	43	
S	1.68 cm.	0.952 cm.	0.30 cm.	0.332 cm.
s x w	118	97.0	66	14.4
P	3.80 mm.	3.328 mm.	2.75 mm.	0.248 mm.
Y	89	73	52	

XXII

Date : 18/7/57

Locality : near Samuelston, East Lothian.

Habitat : Moor with scattered _Quercus_, _Acer_ and _Betula_ -- all rather small and shrubby. Growing with _Agrostis tenuis_, _Deschampsia caespitosa_, _Anthoxanthum odoratum_, _Potentilla erecta_, _Succisa pratensis_ and _Galium saxatile_.

Character	max.	mean	min.	standard deviation
H	55.5 cm.	32.8 cm.	20.5 cm.	7.4 cm.
L	14.6 cm.	10.22 cm.	3.9 cm.	2.70 cm.
B	0.52 cm.	0.336 cm.	0.20 cm.	0.083 cm.
Z	105	77	45	
s/w	1.63	1.496	1.40	0.057
a + f	1.75 mm.	1.375 mm.	1.08 mm.	0.160 mm.
$\frac{a}{a+f}$	0.608	0.5207	0.400	0.049
F	51-55	c, 27	11-15	
Sp	7	4-5	3	
X	123	108	96	
S	1.16 cm.	0.621 cm.	0.17 cm.	0.339 cm.
s x w	149	103.3	70	15.1
P	3.70 mm.	3.002 mm.	2.35 mm.	0.371 mm.
Y	112	78	56	

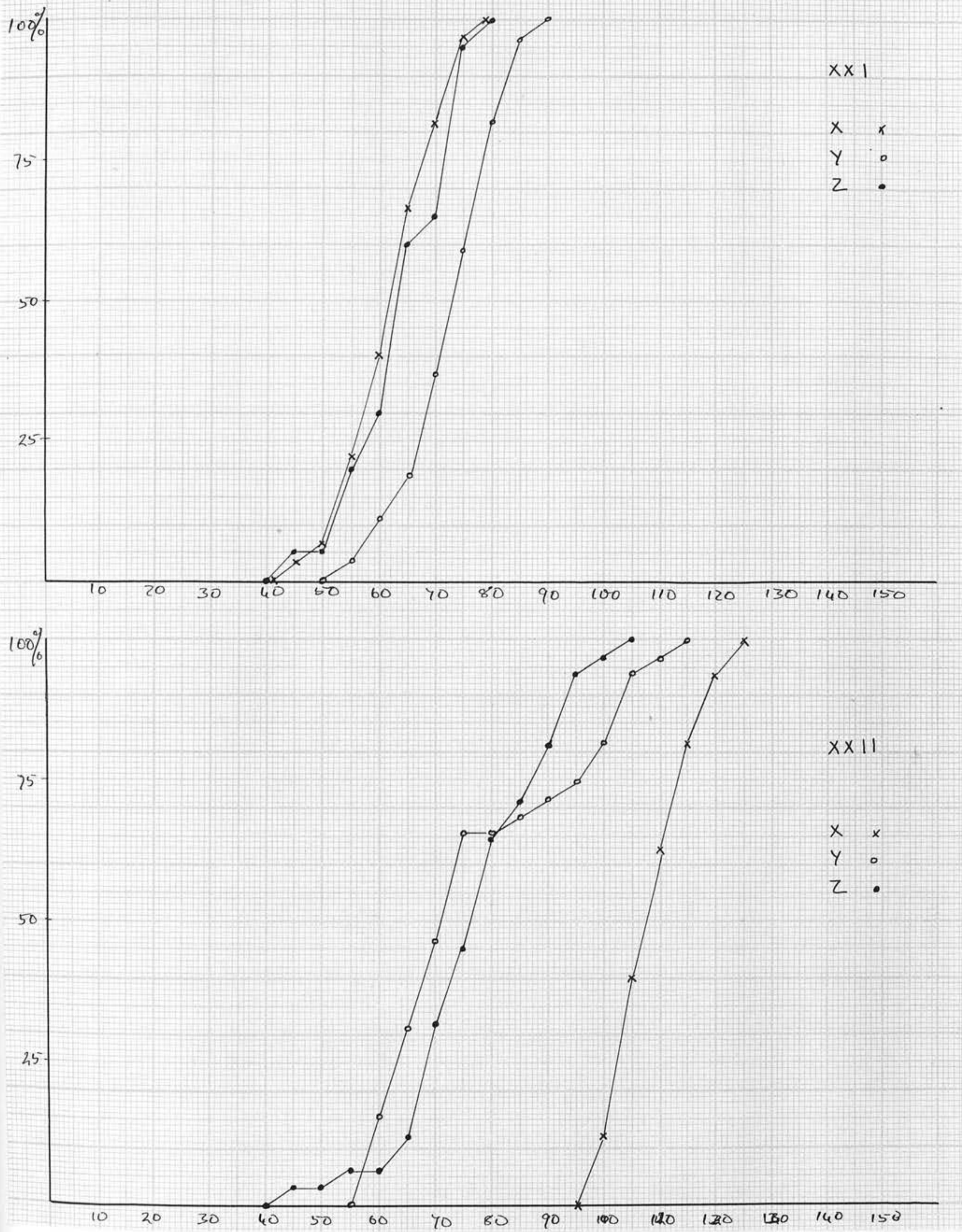
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Fig. 75 a and b

XXIII A

Date : 6/8/57

Locality : near Fintry, Stirlingshire.

Habitat : Damp flush on sttep bank at side of river; facing south. Growing with Juncus acutiflorus, Molinia caerulea, Cirsium palustre, Potentilla erecta, Holcus lanatus and Deschampsia caespitosa.

Character	max.	mean	min.	standard deviation
H	53.0 cm.	39.7 cm.	30.0 cm.	5.9 cm.
L	17.1 cm.	9.78 cm.	7.6 cm.	4.74 cm.
B	0.37 cm.	0.302 cm.	0.20 cm.	0.048 cm.
Z	97	81	68	
s/w	1.58	1.455	1.26	0.068
a + f	1.75 mm.	1.410 mm.	1.10 mm.	0.161 mm.
$\frac{a}{a + f}$	0.576	0.4996	0.385	0.0537
F	41-45	c. 28	16-20	
Sp	6	4	2	
X	124	105	92	
S	1.04 cm.	0.402 cm.	0.16 cm.	0.321 cm.
s x w	142	120.2	93	11.4
P	3.95 mm.	3.31 mm.	2.70 ɱm.	0.272 mm.
Y	112	97	65	

XXIII B

Date : 6/8/57

Locality : near Fintry.

Habitat : Drier ground near XXIII A; steep south slope. Growing with Agrostis tenuis, Holcus lanatus, Anthoxanthum odoratum and Nardus stricta.

Character	max.	mean	min.	standard deviation
H	46.0 cm.	35.2 cm.	25.5 cm.	6.8 cm.
L	19.0 cm.	11.79 cm.	8.5 cm.	2.60 cm.
B	0.41 cm.	0.299 cm.	0.23 cm.	0.055 cm.
Z	94	80	64	
s/w	1.65	1.485	1.30	0.085
a + f	1.81 mm.	1.379 mm.	1.06 mm.	0.179 mm.
$\frac{a}{a + f}$	0.638	0.4385	0.299	0.077
F	41-45	c. 28	16-20	
Sp	6	4-5	3	
X	128	113	88	
S	1.28 cm.	0.446 cm.	0.14 cm.	0.352 cm.
s x w	142	113	75	14.5
P	3.75 mm.	2.975 mm.	2.20 mm.	0.400 mm.
Y	113	87	51	

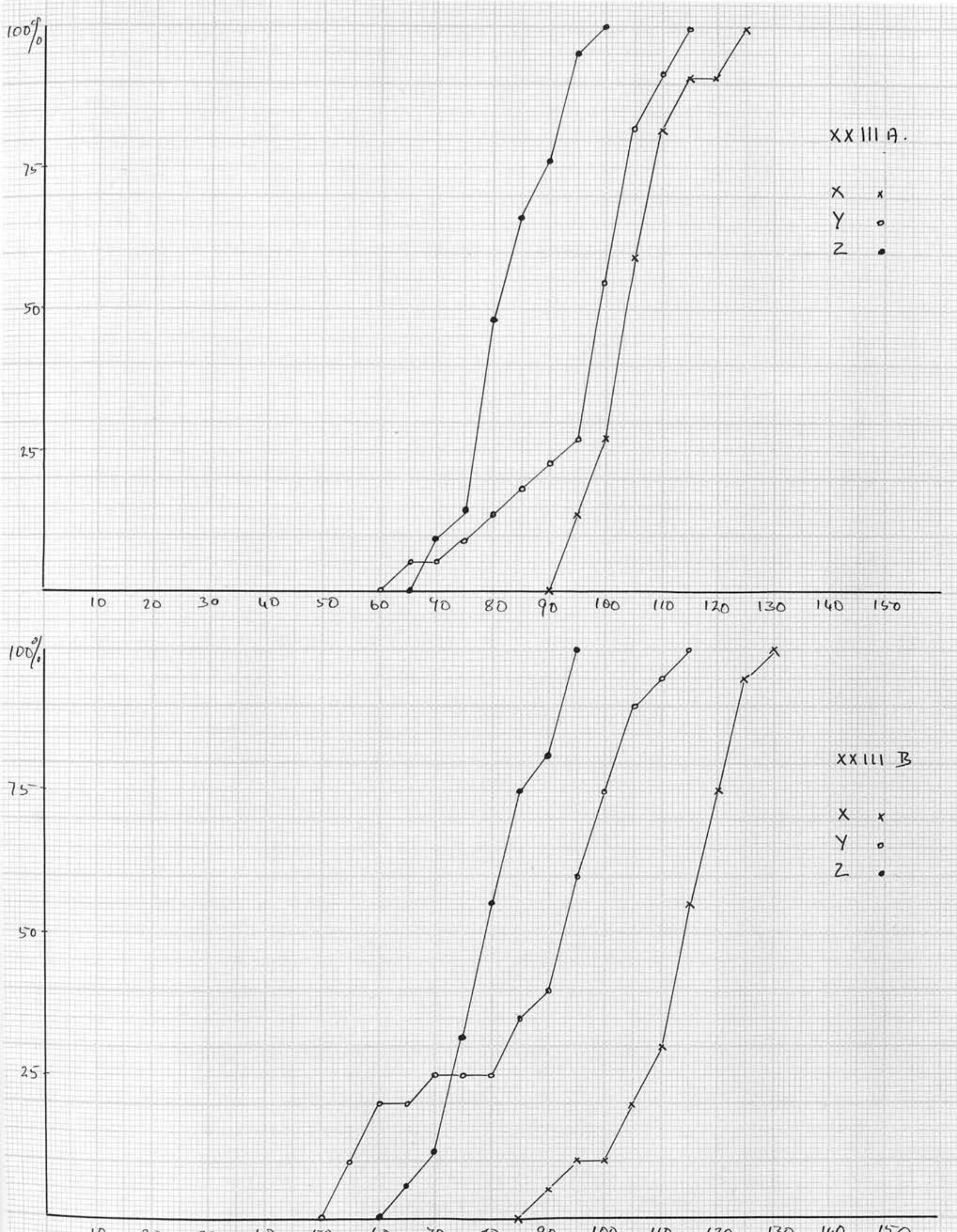

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Fig. 76 a and b

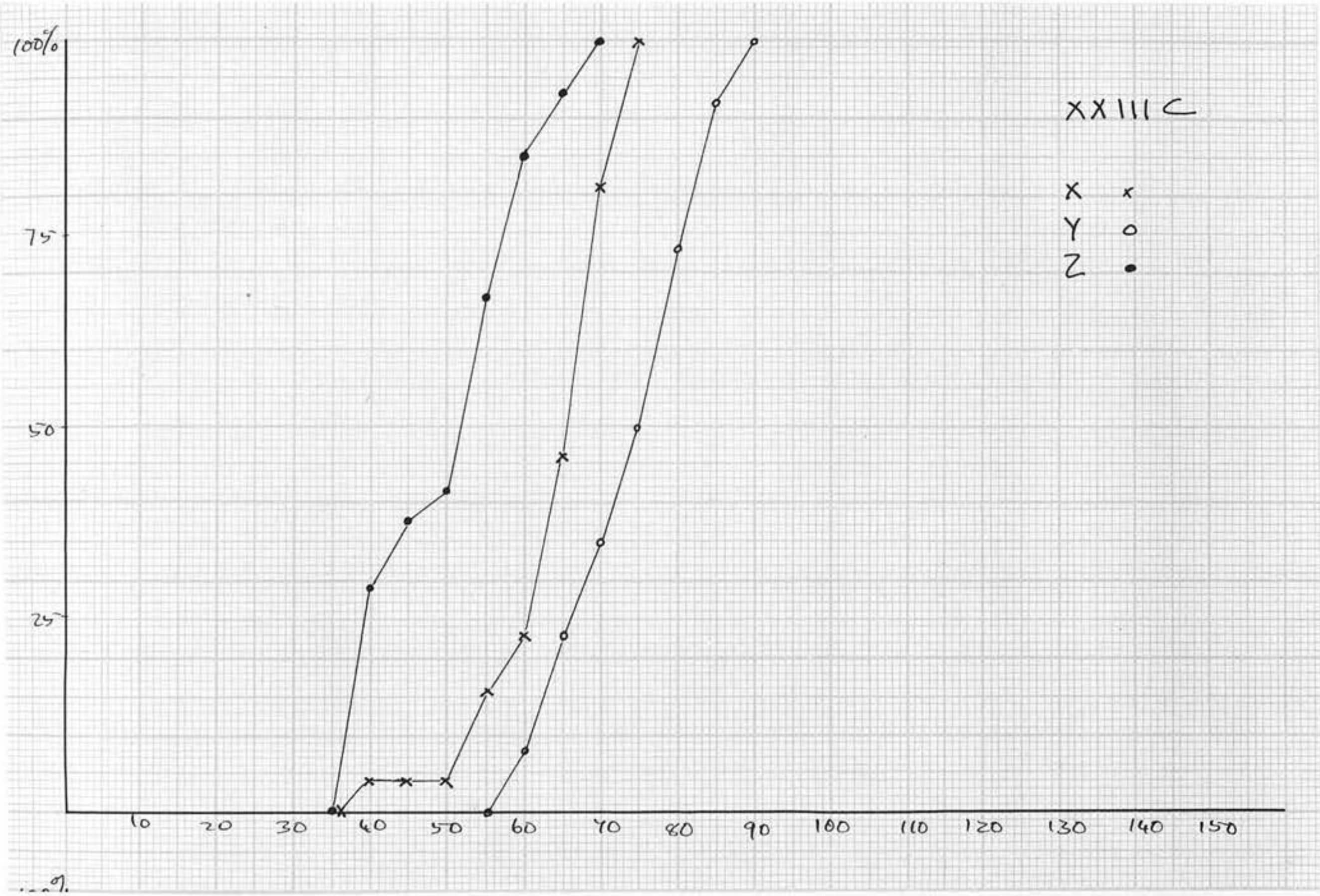
XXIII C

Date : 6/8/57

Locality : Fintry.

Habitat : Dry ground at top of slope above XXIII A and B; pasture, grazed by sheep. Growing with *Agrostis tenuis*, *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Galium saxatile*, *Potentilla erecta* and *Festuca ovina*.

Character	max.	mean	min.	standard deviation
H	24.0 cm.	16.7cm.	9.5 cm.	4.2 cm.
L	10.2 cm.	5.99 cm.	3.5 cm.	1.77 cm.
B	0.30 cm.	0.234 cm.	0.14 cm.	0.041 cm.
Z	68	50	36	
s/w	1.41	1.233	1.08	0.079
a + f	2.51 mm.	1.797 mm.	1.41 mm.	0.236 mm.
$\frac{a}{a + f}$	0.820	0.6914	0.568	0.0572
F	26-30	c. 17	6-10	
Sp	5	3	2	
X	74	64	40	
S	1.35 cm.	0.806 cm.	0.25 cm.	0.302 cm.
s x w	125	101.3	81	10.6
P	4.00 mm.	3.157 mm.	2.60 mm.	0.371 mm.
Y	88	74	59	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XXIII C
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Fig. 77

VIII A

Date ; 2/5/56 Altitude : near sea level.

Locality : Between Longniddry and Port Seton, East Lothian.

Habitat : Dune pasture, slight south slope, campestris.

VIII B

Date : 2/5/56 Altitude : near sea level.

Locality : Between Longniddry and Port Seton.

Habitat : Dune pasture, slight east slope; about 50 yards west of VIII A; campestris.

IX A

Date : 17/5/56

Locality : Silverburn, Midlothian.

Habitat : Pasture, with Festuca ovina and Poa pratensis; grazed by sheep. campestris.

IX C

Date : 17/5/56

Locality : West of Boganlea Reservoir, Midlothian.

Habitat : North-east slope on side of small burn; pasture, passing into community with Calluna; campestris.

X A

Date : 17/5/56

Locality : Bavelaw Quarry, Midlothian.

Habitat : Pasture with Festuca ovina, north-west slope; campestris.

X B

Date; 17/5/56

Locality : South of Balerno, near Threipmuir Reservoir.

Habitat : Under beech trees, at edge of road; 25% or more bare ground; campestris.

X C

Date : 17/5/56

Locality : Threipmuir.

Habitat : Path on east side of road; level, open patch at edge of road, with Festuca rubra and Succisa pratensis; campestris.

X D

Date : 17/5/56

Locality : Threipmuir.

Habitat : Edge of path near X C, but more shaded; Festuca rubra, Succisa pratensis and Juncus squarrosus; congesta.

XI

Date : 22/5/56

Locality : Gullane Point, East Lothian.

Habitat : Dune slack, among dunes just south of Gullane Point, with Festuca rubra, Carex arenaria and Cirsium arvense; campestris.

APPENDIX II.

Tables and outline of calculations of the discriminant function.

PETAL LENGTH (P), SEED SIZE (R) AND CONGESTION INDEX (S) OF THE PLANTS FROM WHICH THE DISCRIMINANT FUNCTION WAS CALCULATED.

a) MULTIFLORA.

P	R	S	Y	P	$R^{\frac{1}{3}}$	S	Y
22	18	8	48	31	27	12	70
19	15	21	55	26	27	10	63
28	23	15	66	16	17	22	55
20	28	11	59	17	24	11	52
25	18	16	59	32	23	14	69
18	14	13	45	27	21	11	59
25	23	7	55	27	23	13	63
20	14	10	44	18	21	7	46
23	15	10	48	19	24	8	51
25	15	11	51	24	24	13	61
12	18	8	38	24	24	10	58
20	20	20	60	24	28	6	58
36	24	8	68	22	24	6	52
30	16	9	55	25	24	10	59
14	14	14	42	24	22	12	58
27	13	16	56	28	22	10	60
23	17	16	56	28	23	6	57
20	20	23	63	24	25	8	57
27	26	17	70	29	21	4	54
21	15	20	56	26	19	11	56
25	24	12	61	26	21	9	56
29	23	12	64	22	20	7	49
24	17	10	51	29	26	14	69
29	33	13	75	34	16	9	59
37	28	16	81	27	31	13	71

$\bar{P} = 24.6$ $\bar{R} = 21.4$ $\bar{S} = 11.8$

b) CONGESTA.

P	R	S	Y	P	R	S	Y
27	19	49	95	42	26	35	103
27	21	37	85	37	28	36	101
34	26	39	99	41	25	37	103
34	19	38	91	31	21	37	89
28	33	39	100	36	21	37	94
29	27	36	92	30	18	38	86
21	26	46	93	31	19	38	88
24	23	39	86	37	26	38	101
31	28	38	97	40	28	37	105
23	25	45	93	41	28	35	104
40	30	44	114	40	23	36	99
36	37	40	114	36	31	38	105
41	37	37	116	39	33	35	107
27	30	41	98	35	22	38	95
29	22	42	93	40	26	36	102
30	34	37	101	37	22	36	95
19	22	41	82	35	25	39	99
27	30	46	103	30	33	25	88
30	30	37	97	33	23	36	92
25	21	47	93	36	22	17	75
38	26	41	105	38	35	37	110
31	19	38	88	36	38	36	110
31	27	36	94	27	27	38	92
29	26	40	95	40	32	42	114
34	25	40	99	31	28	41	100

$\bar{P} = 32.9 \quad \bar{R} = 26.5 \quad \bar{S} = 38.2$

$\Sigma\, P = 2872$ $\quad\Sigma\, P^2 = 87142$ $\quad\Sigma\, PR = 70666$

$\Sigma\, R = 2393$ $\quad\Sigma\, R^2 = 60363$ $\quad\Sigma\, PS = 76706$

$\Sigma\, S = 2503$ $\quad\Sigma\, S^2 = 82153$ $\quad\Sigma\, RS = 62986$

corrected sums of squares and products :

$$\Sigma\,(\bar{P} - P)^2 = \Sigma\, P^2 - \frac{(\Sigma P)^2}{N}$$

$$\Sigma\,(\bar{P} - P)(\bar{R} - R) = \Sigma\, PR - \frac{(\Sigma P)(\Sigma R)}{N}$$

Σp^2, Σpr etc. = corrected sums of squares and products.

$(\Sigma\, P)^2 = 8248384$ $\quad(\Sigma\, P)(\Sigma R) = 6872696$

$(\Sigma R)^2 = 5726449$ $\quad(\Sigma P)(\Sigma S) = 7188616$

$(\Sigma S)^2 = 6265009$ $\quad(\Sigma R)(\Sigma S) = 5989679$

$N = 100$

$\therefore\ \Sigma p^2 = 87142 - 82483.84 = 4658.16$

$\Sigma r^2 = 60363 - 57264.49 = 3098.51$

$\Sigma s^2 = 82153 - 62650.09 = 19502.91$

$\Sigma pr = 70666 - 68726.96 = 1939.04$

$\Sigma ps = 76706 - 71886.16 = 4819.84$

$\Sigma rs = 62986 - 59896.79 = 3089.21$

dp, dr and ds are the differences between the means of P, R and S of <u>congesta</u> and <u>multiflora</u>.

dp = 8.32 ; dr = 5.14 ; ds = 26.38.

discriminant function,= K_1 , K_2 , K_3

$$K_1 \Sigma p^2 + K_2 \Sigma pr + K_3 \Sigma ps = dp$$

$$K_1 \Sigma pr + K_2 \Sigma r^2 + K_3 \Sigma rs = dr$$

$$K_1 \Sigma ps + K_2 \Sigma rs + K_3 \Sigma s^2 = ds$$

$$4658.16 K_1 + 1939.04 K_2 + 4819.84 K_3 = 8.32$$

$$1939.04 K_1 + 3098.51 K_2 + 3089.21 K_3 = 5.14$$

$$4819.84 K_1 + 3089.21 K_2 + 19502.91 K_3 = 26.38$$

this equation is solved by means of matrices to give :

$K_1 = 45.14$ $K_2 = 15.37$ $K_3 = 117.54$

dividing throughout by 15.37 gives :

$K_1 = 2.937$, $K_2 = 1.000$, $K_3 = 7.647$

these are then multiplied by two, and reduced to the nearest whole number to give :

$K_1 = 6$

$K_2 = 2$

$K_3 = 15$

INDEX VALUES OF PETAL LENGTH (p), SEED SIZE (r) AND CONGESTION INDEX (s), AFTER THE APPLICATION OF THE DISCRIMINANT FUNCTION.

a) MULTIFLORA.

p	r	s	Y'	p	r	s	Y'
132	36	120	288	186	54	180	420
114	30	315	459	156	54	150	360
168	46	225	439	96	34	330	460
120	56	165	341	102	48	165	315
150	36	240	426	192	46	210	448
108	28	195	331	162	42	165	369
150	46	105	301	162	46	195	403
120	28	150	298	108	42	105	255
138	30	150	318	114	48	120	282
150	30	165	345	144	48	195	387
72	36	120	228	144	48	150	342
120	40	300	460	144	56	90	290
216	48	120	384	132	48	90	270
180	32	135	347	150	48	150	348
84	28	210	322	144	44	180	368
162	26	240	428	168	44	150	362
138	34	240	412	168	46	90	304
120	40	345	505	144	50	120	314
162	52	255	469	174	42	60	276
126	30	300	456	156	38	165	359
150	48	180	378	156	42	135	333
174	46	180	400	132	40	105	277
144	34	150	328	174	52	210	436
174	66	195	435	204	32	135	371
222	56	240	518	162	62	195	419

b) <u>CONGESTA</u>.

p	r	s	Y'	p	r	s	Y'
162	58	735	935	252	52	525	729
162	42	555	759	222	56	540	718
204	52	585	841	246	50	555	851
204	38	570	812	186	42	555	738
168	66	585	819	216	42	555	813
174	54	540	768	180	36	570	786
126	52	690	868	186	38	570	794
144	46	585	775	222	52	570	844
186	56	570	812	240	54	555	849
138	50	675	863	246	54	525	825
240	60	660	960	240	46	540	826
216	74	600	890	216	62	570	848
246	74	555	875	234	66	525	825
162	60	615	837	210	44	570	824
174	44	630	848	240	52	540	832
180	68	555	803	222	44	540	806
114	44	615	773	210	50	585	845
162	60	690	912	180	66	375	621
180	60	555	795	198	46	540	784
150	42	705	897	216	44	255	515
228	52	615	895	228	70	555	853
186	38	570	794	216	76	540	832
186	54	540	780	162	54	570	786
174	52	600	826	240	64	630	934
204	50	600	854	186	56	615	857

Plate 1. Habitat of populations II F (i) - (iv) in Glen Lyon. (iv) was collected on the level ground at the left of the photograph, (iii) a & b on the slope, (ii) in the band of _Juncus_, and (i) in the bog at the right.

PLATES 2 - 16.

DISSECTIONS OF FLOWERS.

The floral parts are arranged in the following order, from left to right :

outer perianth segment

inner perianth segment

stamen

capsule segment

The seed is attached to the main photograph, when it is available.

All photographs are x 15.

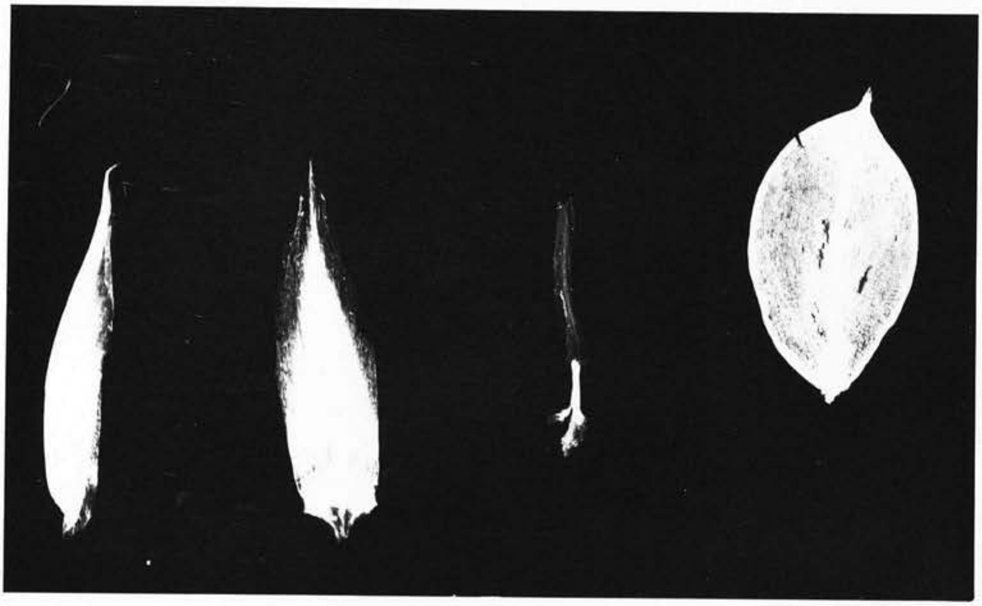


Plate 2. campestris.

Plate 3. pallescens.

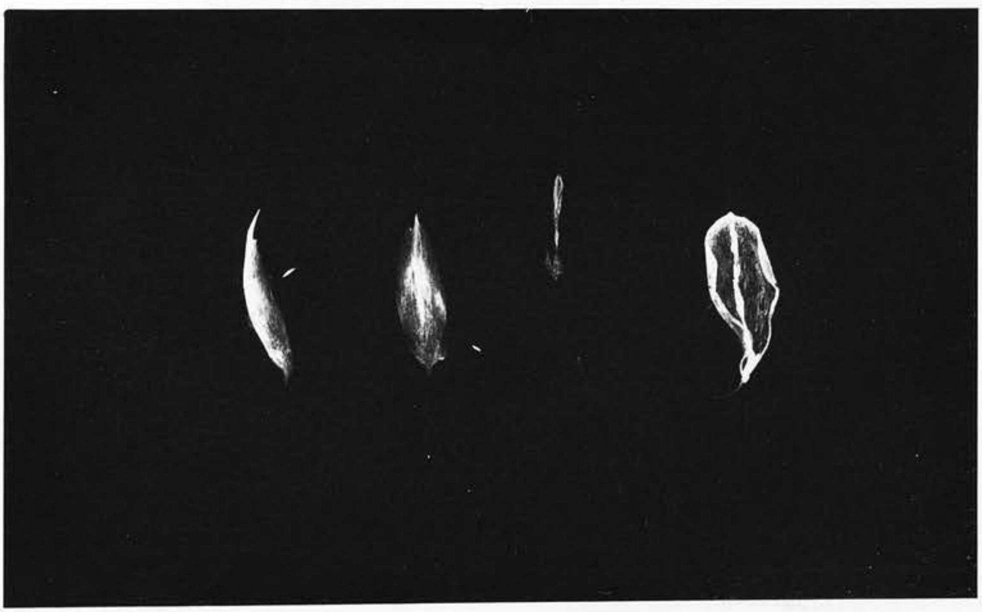


Plate 4. <u>multiflora</u>.

Plate 5. <u>congesta</u>.

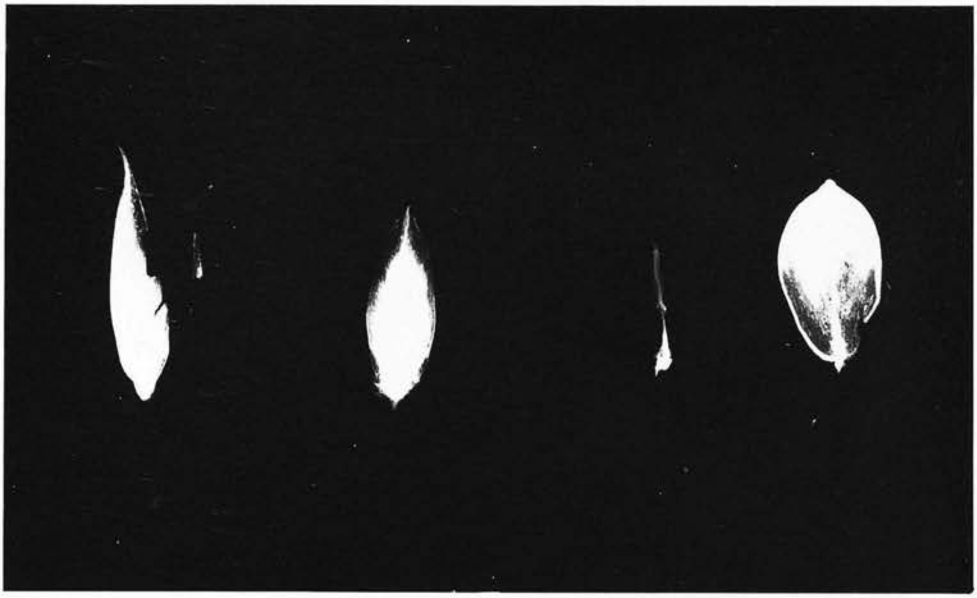
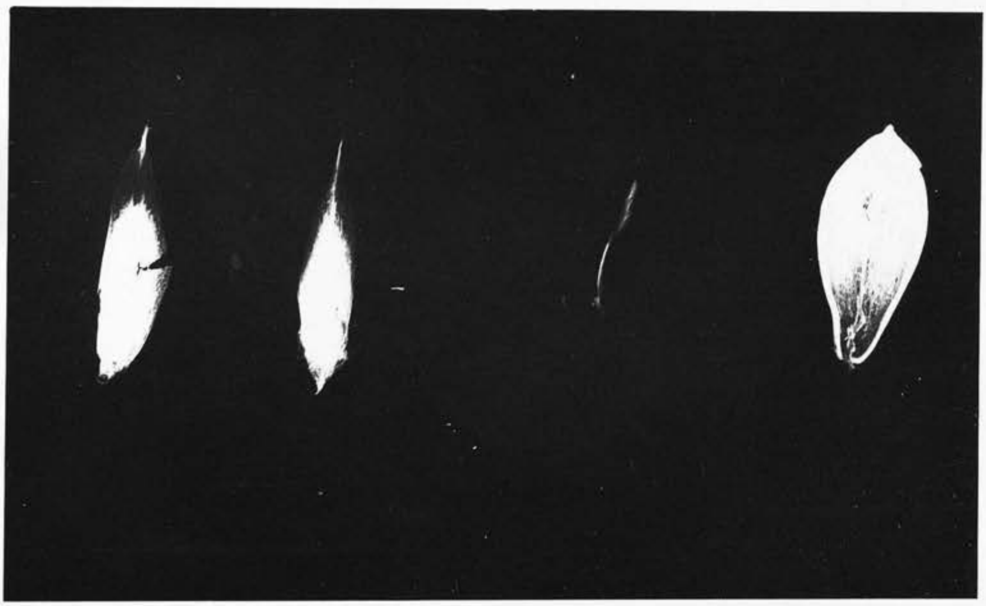
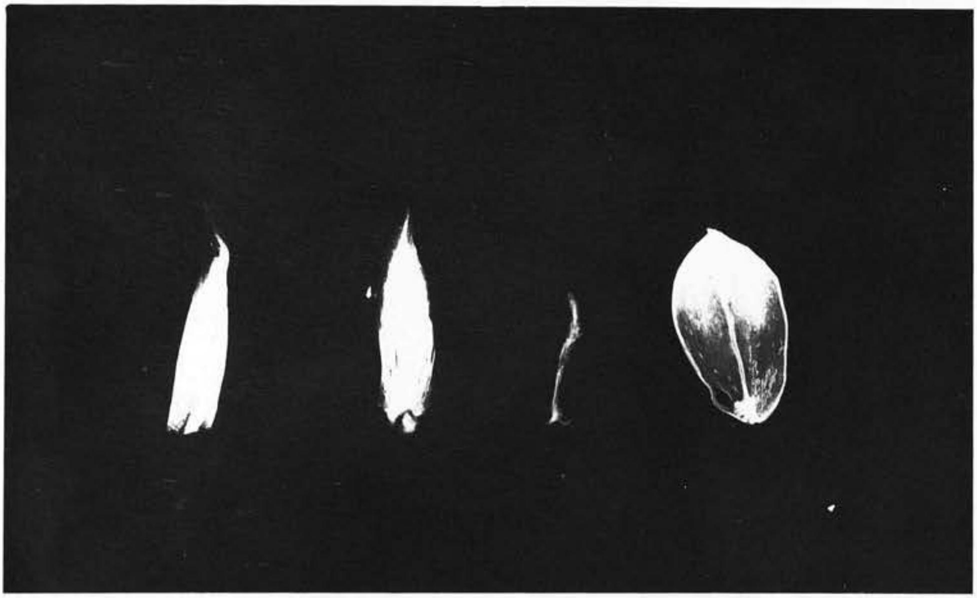


Plate 6. sudetica.

Plate 7. frigida.

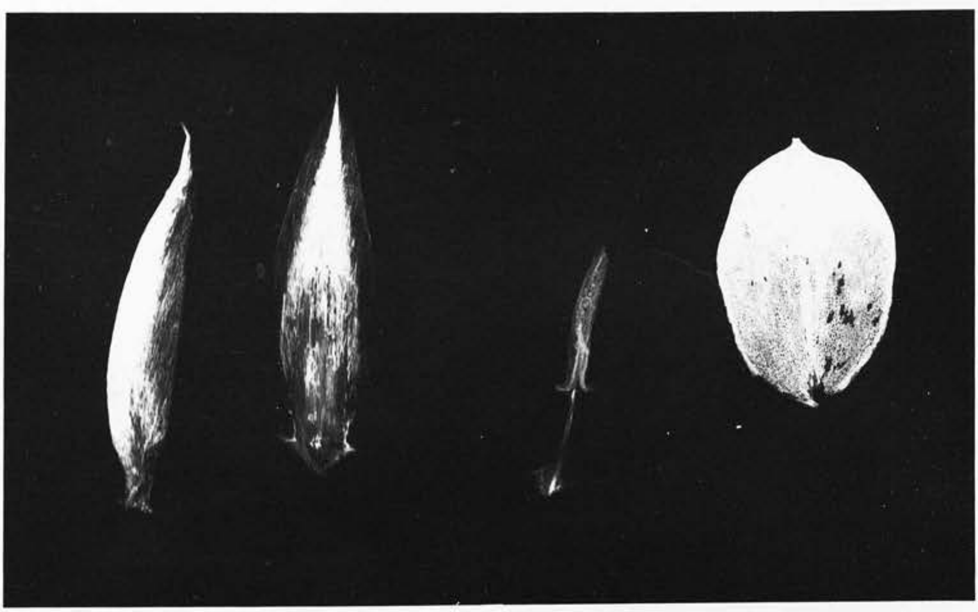




olig

Plate 8. <u>oligantha</u>.

Plate 9. <u>capitata</u>.



cap

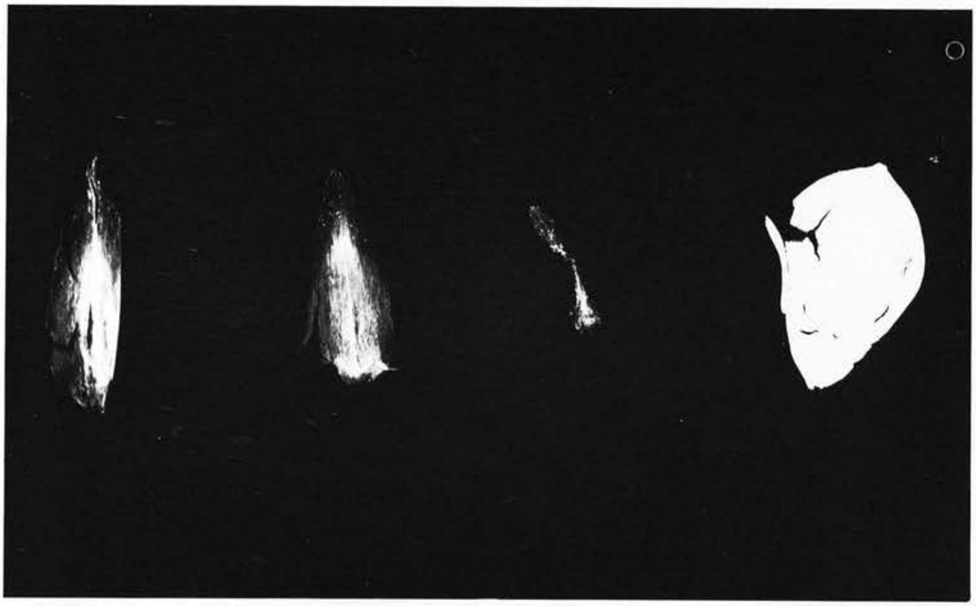
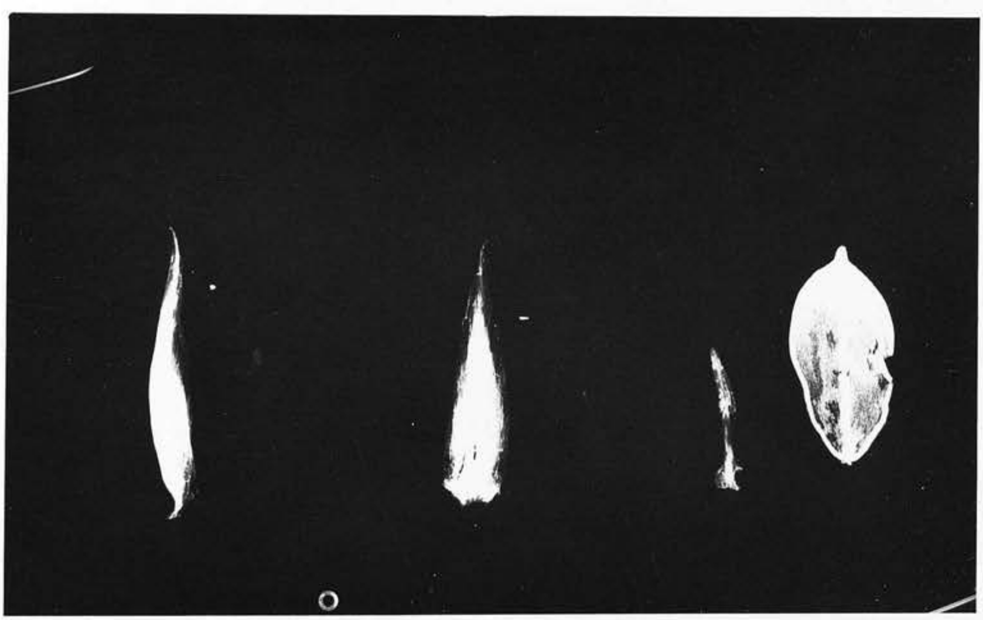
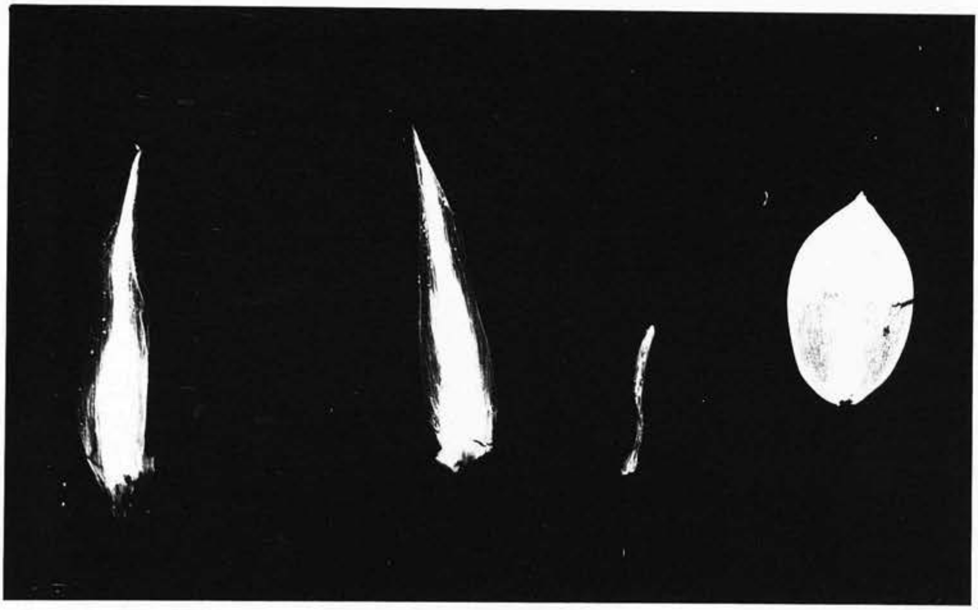


Plate 10. migrata.

Plate 11. australasica.

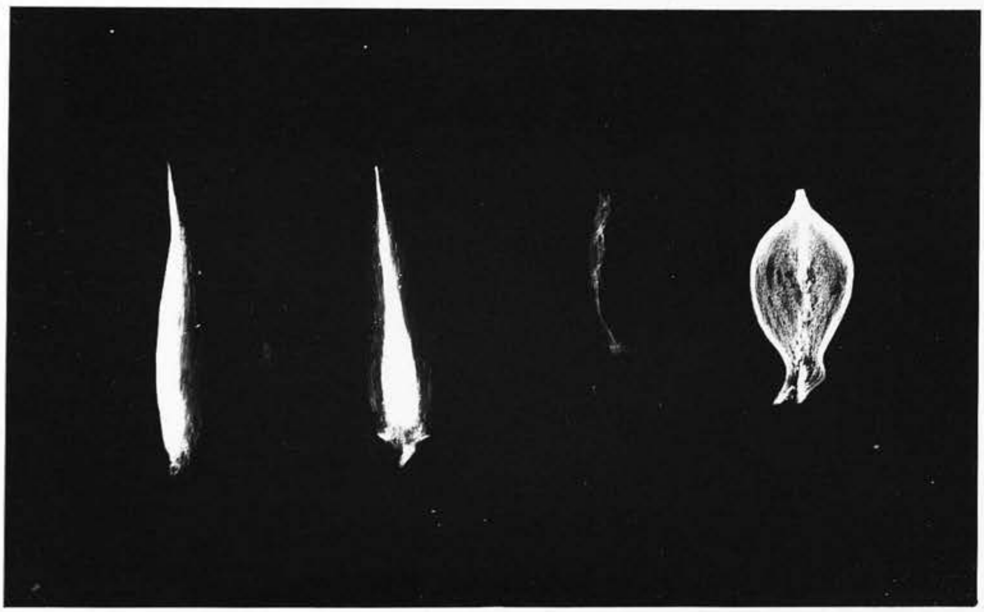




banks.

Plate 12. banksiana.

Plate 13. picta.



picta

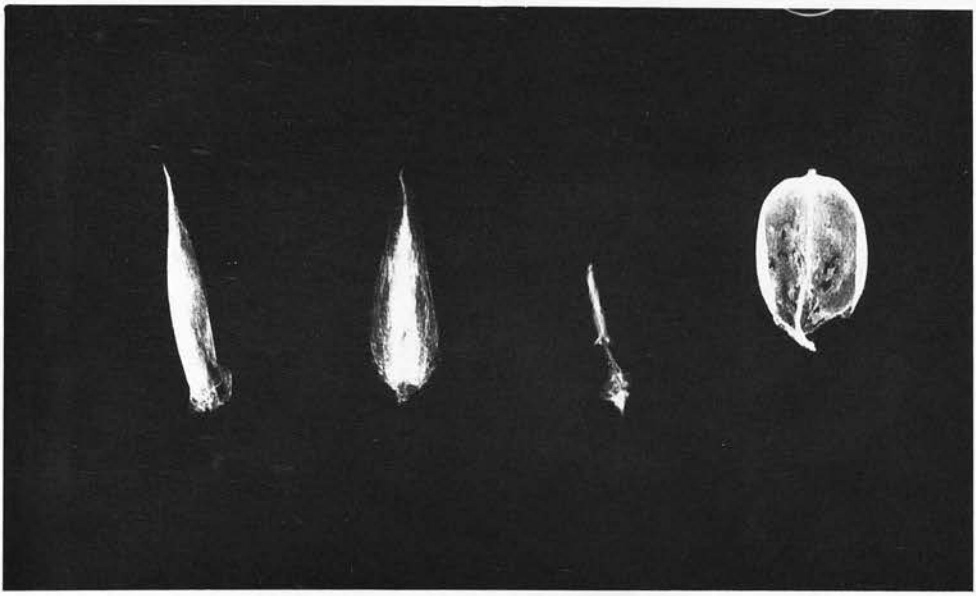


Plate 14. bulbosa.

Plate 15. echinata.

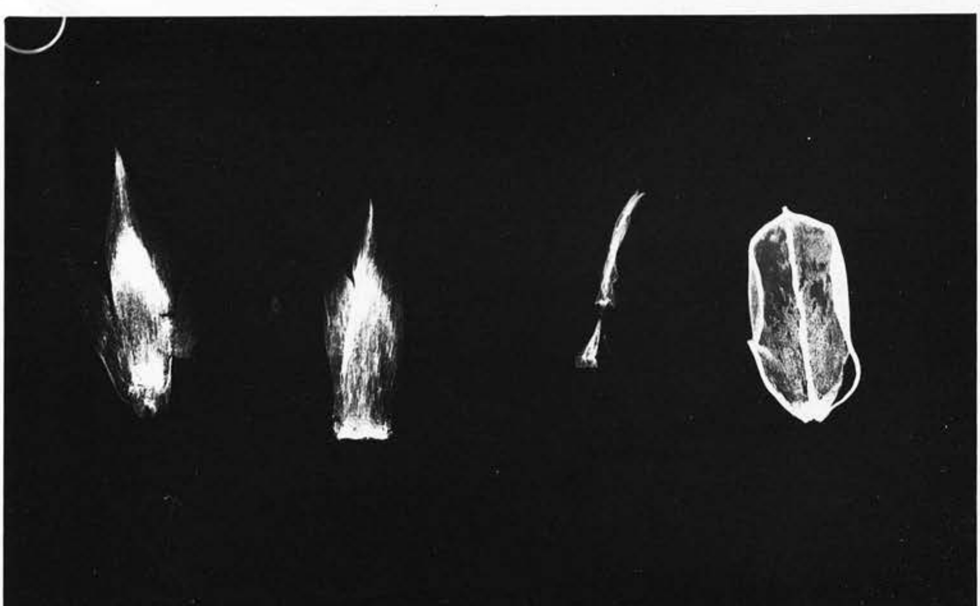
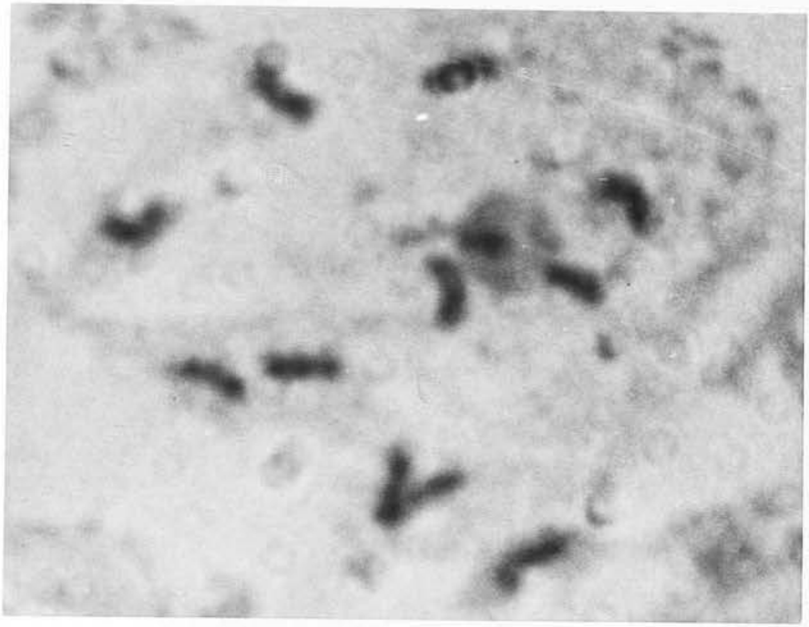


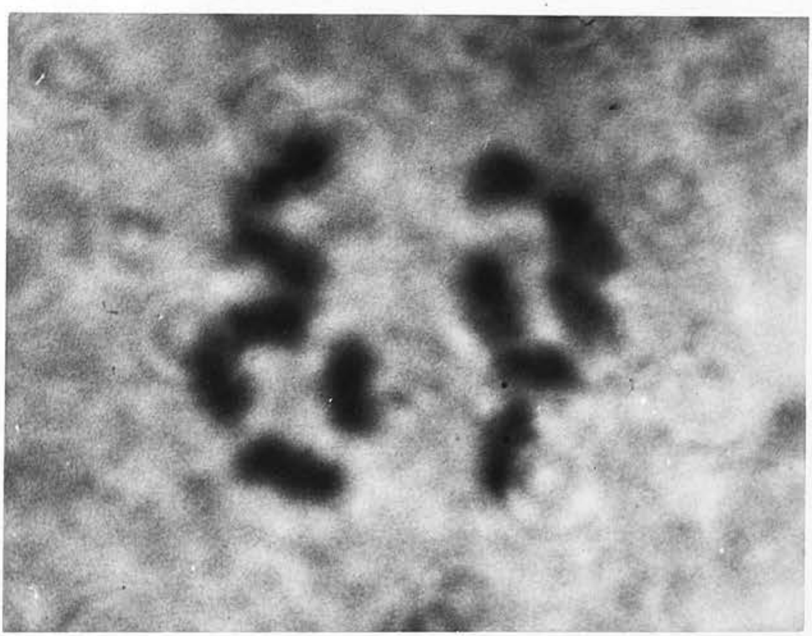
Plate 16. comosa.



10 μ

Plate 17. <u>campestris</u>, 2n = 12.

Plate 18. <u>campestris</u>, 2m = 12.



10 μ

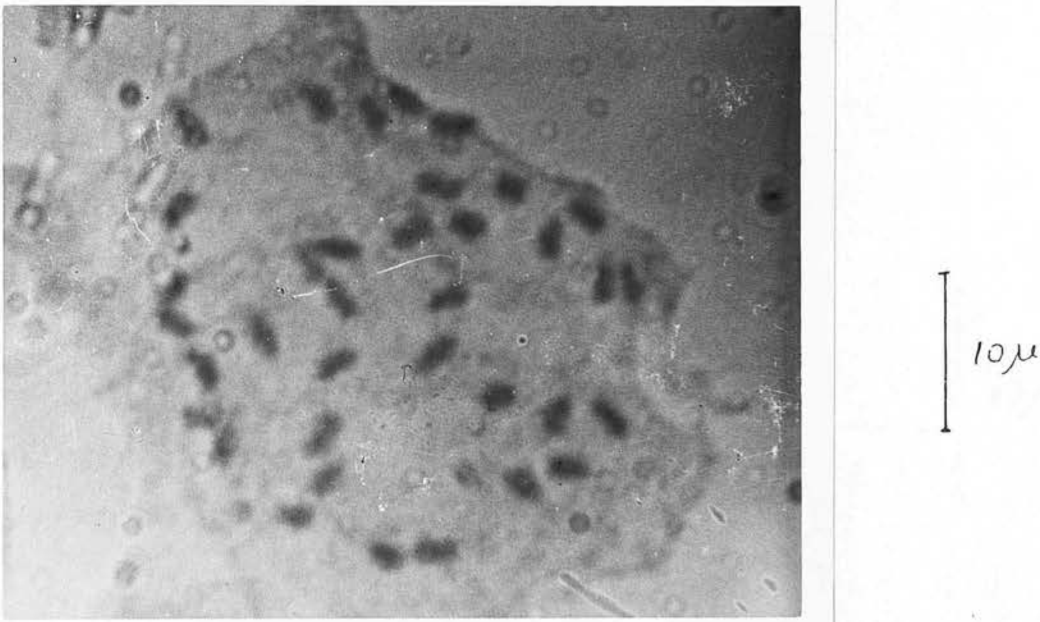
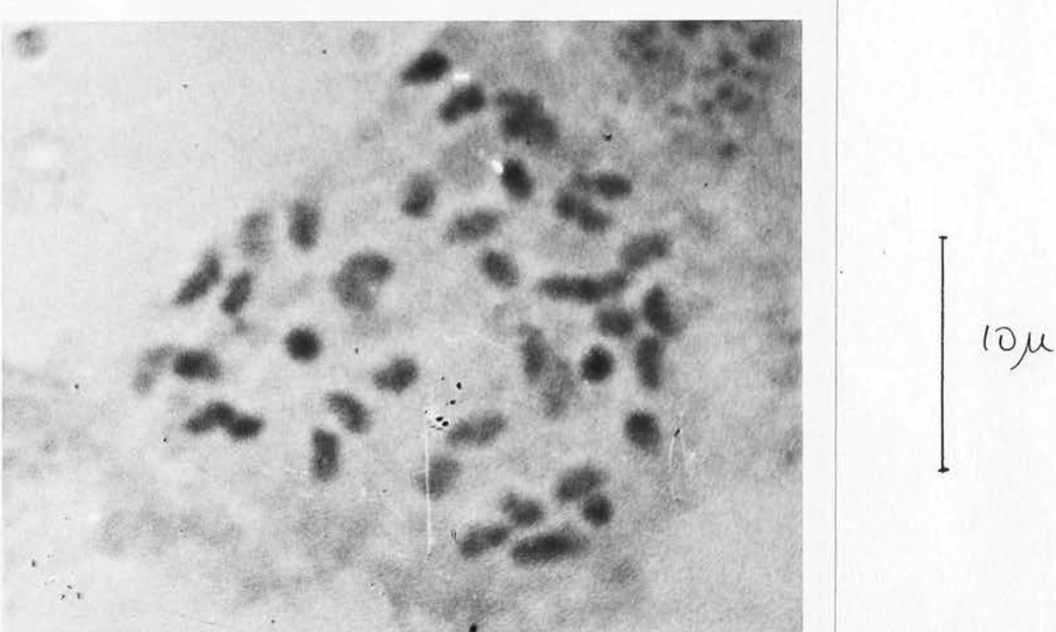
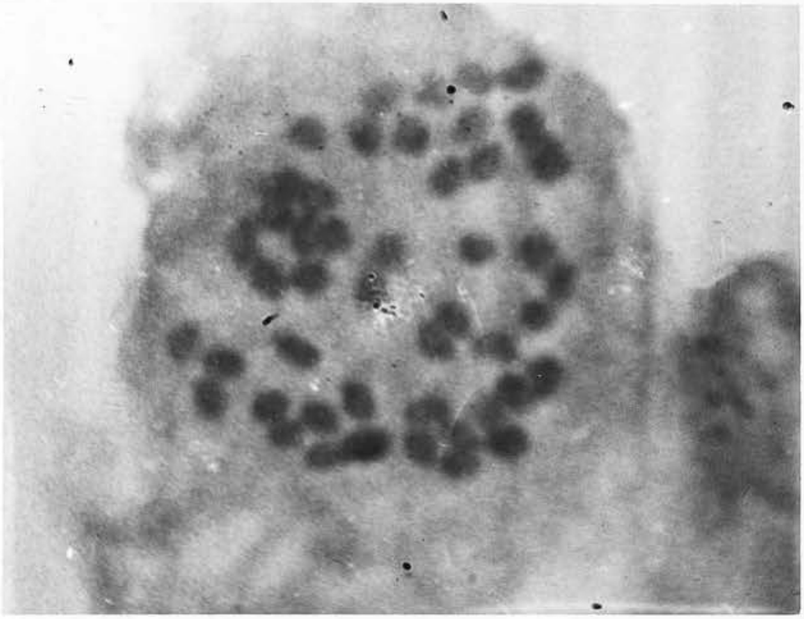


Plate 19. multiflora, 2n = 36.

Plate 20. multiflora x congesta, 2n = 42.

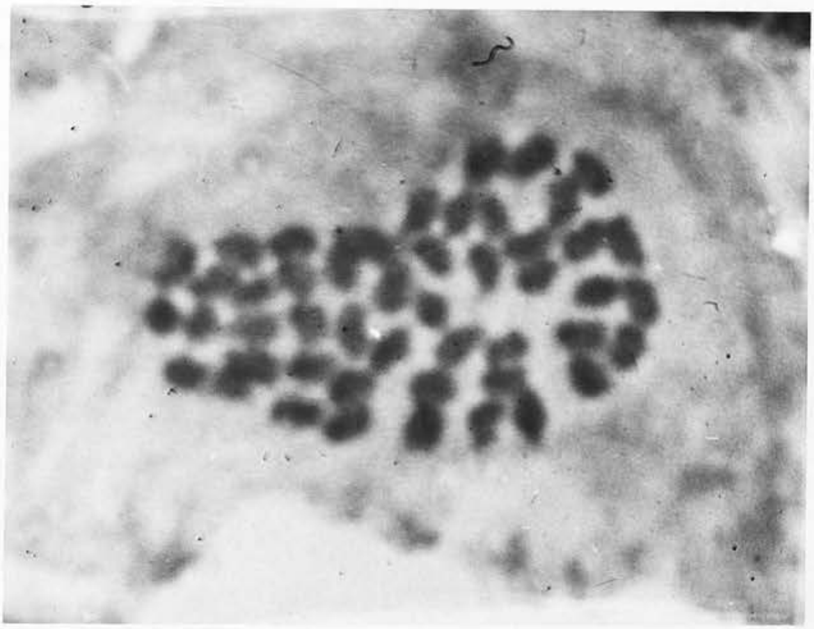




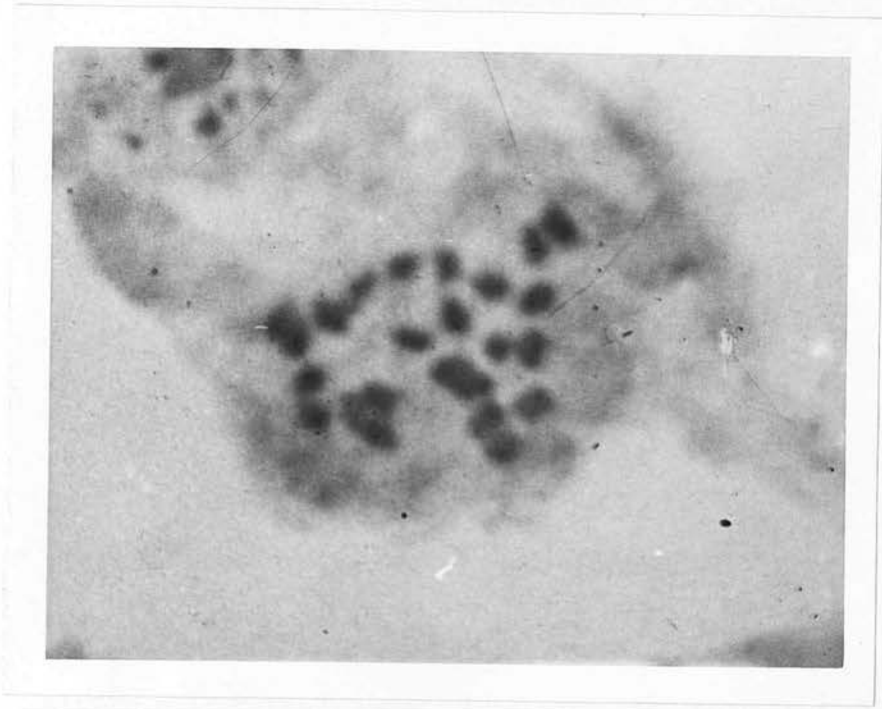
10µ

Plate 21. congesta, 2n = 48.

Plate 22. congesta, 2n = 48.



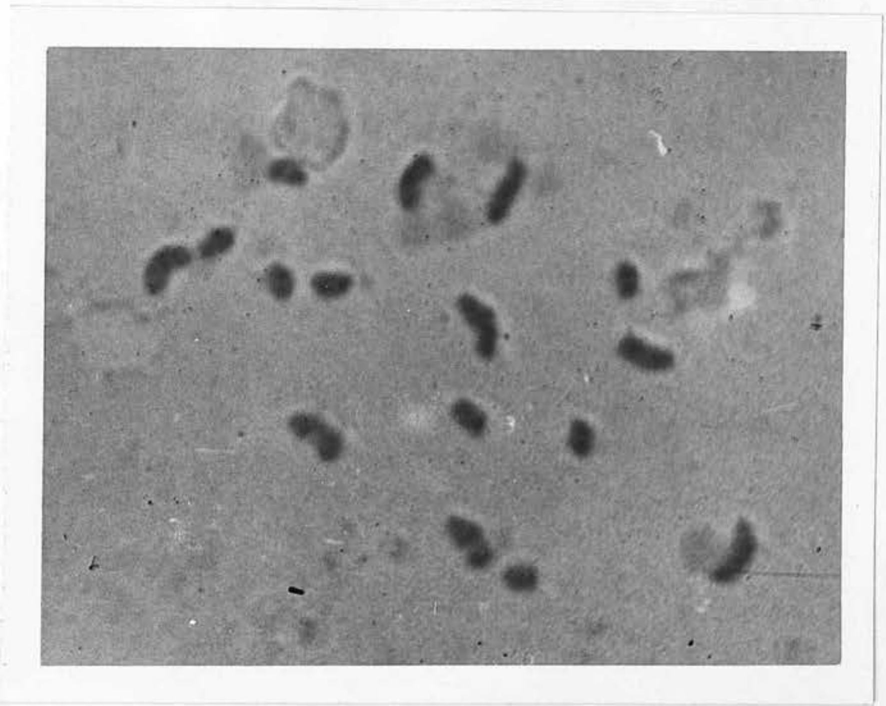
10µ



10μ

Plate 23. L. forsteri, 2n = 24.

Plate 24. migrata, 2n = 16.
note 8 large and 8 small chromosomes.



10μ